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The American Midland Naturalist

Founded by J. A. Nieuwland, C. S. C.
Edited by Theodor Just

CONTENTS

Symposium on Paleobotanical Taxonomy

Introduction — Theodor Just 257

Fossil Algae

Algae of the Pre-Cambrian and Early Paleozoic — Carroll L. Fenton 259
Late Paleozoic Algae of North America — J. Harlan Johnson 264
Fossil Charophyta — Raymond E. Peck 275
Algae as Ecologic Indicators — Waldo S. Glock 279
Fossil Symbiotic Algae in Comparison with Other Fossil and Living Algae—Maxim K. Elias 282

Fossil Bryophytes and Vascular Plants

The Relative Value of Taxonomic Characters — Theodor Just 291
Cenozoic and Mesozoic Bryophytes of North America — William C. Steere 298
The Taxonomic Treatment of the Fern-Pteridosperm Complex — Norman W. Radforth 325
Studies in the Trigonocarpales. Part II. Taxonomic Problems and a Revision of the Genus Pachytesta — J. H. Hoskins and A. T. Cross 331
The Role of Wood Anatomy in Phylogeny — Oswald Tippo 362
Taxonomy of Tertiary Flowers and Herbaceous Seeds — Maxim K. Elias 373

A Revision of Phacelia Sect. Euglypta — John Thomas Howell 381
Ficus in Florida — I. Australian Species — Mary F. Barrett 412
Development of Prairie at Iowa Lakeside Laboratory — W. A. Anderson 431
Observations on the Desert Gypsum Flora of Southwestern Texas and Adjacent New Mexico — U. T. Waterfall 456
Observations on the Biology of the Snail Lymnaea stagnalis appressa During Twenty Generations in Laboratory Culture — Lowell E. Noland and Melbourne R. Carriker 467
Incidence of Worm Parasites in Minnesota Mustelidae and Host Lists and Keys to North American Species — Arnold B. Erickson 494
Book Reviews 510

Vol. 36 September 1946 No. 2

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CONTENTS

Introduction—*Theodor Just* 257

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Late Paleozoic Algae of North America—*J. Harlan Johnson* 264
Fossil Charophyta—*Raymond E. Peck* 275
Algae as Ecologic Indicators—*Waldo S. Glock* 279
Fossil Symbiotic Algae in Comparison with Other Fossil and Living Algae —*Maxim K. Elias* 282

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The Relative Value of Taxonomic Characters—*Theodor Just* 291
Cenozoic and Mesozoic Bryophytes of North America—*William C. Steere* 298
The Taxonomic Treatment of the Fern-Pteridosperm Complex —*Norman W. Radforth* 325
Studies in the Trigonocarpales. Part II. Taxonomic Problems and a Revision of the Genus Pachytesta— *J. H. Hoskins* and *A. T. Cross* 331
The Role of Wood Anatomy in Phylogeny—*Oswald Tippo* 362
Taxonomy of Tertiary Flowers and Herbaceous Seeds—*Maxim K. Elias* 373

Introduction

Theodor Just

The two groups of papers here published as a unit under the general heading of *Paleobotanical Taxonomy* were presented at the first post-war meetings of the American Association for the Advancement of Science, held on March 29-30 in St. Louis, Mo., under the auspices of the Paleobotanical Section of the Botanical Society of America. In organizing these symposia, the writer in his present capacity as secretary of this section enjoyed the full cooperation of its members and participants but was materially assisted by Dr. M. K. Elias, Nebraska Geological Survey, who planned and arranged the first group of papers dealing with *Problems in the Study of Fossil Algae.* Following the suggestion of several contributors to publish these papers together, they appear here with the consent of all concerned. It is hoped that they will be found useful as indicators of our present knowledge of certain groups and that they may also function as possible catalyzers for future work. For it is abundantly clear that much remains to be done before many paleobotanical problems can be resolved to the satisfaction of all, e.g., geologists, botanists of different interests and others.

Obviously symposia of this and similar character can never take the place of exhaustive reference works of highly specialized type such as the *Fossilium Catalogus, Plantae* (as far as published), the classical textbooks in the field, monographs, etc. Limitations of space and other factors prevent such comprehensive enterprises at the outset. Thus whole groups, such as the fungi, are here omitted and the reader is referred to the customary sources (articles on Fungi Fossiles, pp. 125-126 in G. C. Ainsworth and G. R. Bisby, *A Dictionary of the Fungi*, 2. ed. Kew, 1945 and J. Pia, Fungi, pp. 112-136 *in* M. Hirmer, *Handbuch der Palăobotanik*, vol. 1, Munich, 1927).

Likewise many other groups scarcely receive mention in this symposium. However the problems encountered in their study are sufficiently akin to those discussed by the contributors of this symposium that they are covered at least in character, if not by actual treatment.

The nomenclature of living plants may, in the opinion of many, be far from its desired state of complete stability but it is certainly much nearer that goal than is the nomenclature of fossil plants. Since the latter is the main concern of a special committee of the Paleobotanical Section whose aims have been clearly stated elsewhere (J. M. Schopf, Chronica Botanica 7(5): 226-227, 1942), only isolated cases are treated here.

Microfossils have lately been studied with increased vigor and interest, both from a geological as well as a botanical viewpoint. Again certain aspects of "micropaleobotany" have recently been critically summarized and references to some of these sources must suffice in this connection (for lower algal groups see H. Kufferath, *Revue de quelques travaux récents sur les microfossiles*, Bull. Soc. Roy. Bot. Belg. 73(1/2): 225-228, 1940-1941, and the numerous papers by Joaquín Frenguelli in Revista del Museo de La Plata, N. S., Sec. Pal. and Notas del Museo de La Plata, etc.; for spores, pollen and other microfossils see J. M. Schopf, L. R. Wilson, and Ray Bentall, *An Annotated Synopsis of Paleozoic Fossil Spores and the Definition of Generic Groups*, Illinois State Geological Survey, Report of Investigations 91: 73 pp., 3 pls., and since 1943 *Pollen Analysis Circular*, now known as *Pollen and Spore Circular*).

In the light of these meliorating circumstances and the inherent difficulties attending paleobotanical investigations the serious reader will be no more expectant of final results in paleobotany than he will be of such in many other branches of botanical endeavor. Rather he will note with satisfaction that real progress in paleobotany is being made, though perhaps on a less spectacular scale than in other fields.

Algae of the Pre-Cambrian and Early Paleozoic

Carroll Lane Fenton

Introduction

The algae form a diversified array of organisms traditionally regarded as plants and placed in the phylum of thallophytes. Other systems of classification, however, divide them among two to three kingdoms and increase the number of phyla to as many as ten. Five of these are known as fossils in Silurian and earlier rocks, while one of these five—the Nematophyceae—apparently has been extinct since the Devonian.

This paper reviews the characteristics of these five phyla as they are developed among pre-Cambrian and early Paleozoic fossils. Special attention is given to stromatolites and branched structures assigned to the red algae, since these are of major importance in the fossil record, yet have been widely misunderstood.

Cyanophyceae (Blue-green Algae)

This group includes some of the oldest, as well as some of the most convincing algal fossils known from early formations. Thus minute tubules in the Archean of the Lake Superior region were found by Miss Tilden to "resemble very closely" certain existing filamentous genera (Gruner 1923, 1925). Replaced cells and filaments in Proterozoic deposits of Biwabik and early Huronian age closely resemble such modern types as *Inactis* and *Microcoleus* (Gruner 1922, Tilden 1935, p. 5). *Corycinium enigmaticum* from the Pre-Cambrian of Finland (Sederholm 1910, 1925) leaves little doubt of its algal nature, though it may not be a member of the Nostocaceae, as its form suggests. The Ordovician *Gloeocapsomorpha* (Zalessky 1928; Seward 1933, p. 105) consists of yellow bodies .01-.08 mm. in length, each containing several groups of cells which apparently were embedded in a mucilaginous matrix. Though comparable to *Gloeocapsa* in appearance, these fossils have been placed in the Protophyceae, a group based upon this genus but now used as a resting place for varied fossil cyanophytes whose relationships to modern forms have not been fully ascertained.

Outstanding among carbonized remains of algae are those described by Walcott (1919) from the middle Cambrian Burgess Shale of southeastern British Columbia. Of these, the filamentous *Marpolia spissa* closely resembles the modern *Schizothrix* (Walton 1923) and was placed in the Oscillatoriaceae by Pia (1927, p. 35). Some of the carbon films called *Morania* also seem to be blue-greens, though M. (?) *frondosa* must be regarded as a brown alga.

Following the work of Black (1933, p. 171) many carbonaceous laminae and layers found in Pre-Cambrian and early Paleozoic formations may be recognized as algal mats which grew during periods of reduced deposition but

died when sediment again became abundant (Fenton 1943, p. 85). Since no deposits containing cells or filaments have been examined, it is impossible to say whether or not those algal mats were formed by cyanophytes, though such origin seems probable.

Equally puzzling are impressions of the type called *Rivularites*. According to the interpretation of White (1929, p. 41), this supposed fossil is the impression of a basal mat or carpet like that possessed by colonies of *Rivularia*. Currents acting upon the floating filaments caused the carpet to be wrinkled. Unfortunately, many marine impressions comparable to *Rivularites* are found in formations which show no other evidence of strong water currents during their deposition. It also is difficult to separate *Rivularites* from small symmetrical ripple marks of irregular pattern, so that the existence of this form-genus in early sediments is no more than a possibility.

The Porostromata, including such genera as *Girvanella, Epiphyton, Pachytheca* and *Sphaerocodium*, are calcareous algal masses which have recognizable microscopic structure, commonly arranged in radial fashion. The fossils range from tiny spheroids to biscuit-shaped lumps as much as 20 cm. in diameter; in some formations they surround oolitic grains or pebbles, as do certain modern algal structures. Members of the group range from Cambrian to Devonian in age.

Largely because of their gross resemblance to *Girvanella*, calcareous algae of the type called stromatolites or spongiostromes have commonly been considered as members of the Cyanophyceae. In this paper, however, they are referred to the red algae and are discussed under that head.

Chlorophyceae (Green Algae)

This phylum includes a considerable number of stalked or branched calcareous types which are well preserved as fossils. Among the oldest is *Palaeoporella*, whose broken branches form limestones in the Baltic region (Hadding 1933, p. 21). The genus appears in the Cambrian and reaches its greatest development in the Ordovician. *Dimorphosiphon, Primicorallina* and *Cyclocrinus* are well-known Ordovician genera. It seems probable that careful search will reveal many other deposits in which segments of calcareous green algae are important constituents.

It has been suggested that *Oldhamia* (*Murchisonites*) *occidens* Walcott, of the Lower Cambrian, is an impression made by stranded green algae comparable to *Halimeda* (Fenton 1943, p. 87). If this suggestion is correct, the fossil carries the Cyanophyceae back to the beginning of the Paleozoic.

Phaeophyceae (Brown Algae)

The existence of brown algae in early formations has not been proved, though it seems virtually certain that *Morania frondosa* Walcott, of the middle Cambrian, and the Ordovician *Sphenophycus angustifolius* (Hall) belong in this phylum. The latter species shows the tip of a sturdy stipe to which narrow laminae are attached, in the manner of the modern *Postelsia*.

Reasons have been given for classing *Beltina* as a brown algae (Fenton and Fenton 1937, p. 1949; Fenton 1943, p. 84), although it originally was de-

scribed as a crustacean. This conclusion is based upon form and position of carbonized fragments in comparison with those of modern *Ascophyllum* and *Fucus*, not upon microstructure. This is lacking from all known examples of *Beltina*, which are carbonaceous films.

Nematophyceae (Nematophytales)

This group was established by Lang (1937) for the fossils variously known as *Prototaxites*, *Nematophycus* or *Nematophyton*, as well as for structures which may represent their leaflike or laminar expansions, named *Nematothallus* by Lang.

Originally described as a relative of the yews, *Prototaxites* or *Nematophyton* consists of long stalks as much as two feet in diameter, each composed of relatively thick tubes without cross partitions. Found in Silurian and Devonian strata, these fossils were for years regarded as remains of kelplike stipes comparable to that of the living *Lessonia*, a dichotomously branched brown alga found near shores in the southern Pacific (Kräusel 1936). Lang, however, supports Dawson's original opinion that *Nematophyton* grew on land, while Seward (1933, p. 120) thinks that it "probably grew on swampy ground and must have reached the dimensions of a tree." In spite of this, Chapman (1941, p. 274) considers it to have so many features in common with algae as to be properly included with them. He regards Lang's *Nematothallus* as the photosynthetic and perhaps reproductive lamina of *Nematophyton*.

Little can be said for the opinion, once widely held, that early Paleozoic tubes and casts of the type called fucoids in paleontologic literature are traces of brown algae. Some of the fossils appear actually to be casts of compressed or partly withered stipes; some probably represent red algae; many are filled burrows or trails made by animals. Some of these last show marks of appendages and are essentially like structures which, in younger formations, have been attributed to crabs and other crustaceans.

Rhodophyceae (Red Algae)

The Solenoporaceae, which most authors regard as undoubtedly red algae, are spheroidal or biscuit-shaped calcareous masses which appear in the Ordovician and continue to the Jurassic. They bear a general resemblance to *Lithothamnion* in both form and internal structure, though in some species the cross walls are not well developed. Ecologically, if not systematically, *Solenopora* and related generic types have been accepted as predecessors of *Lithothamnion* by even such cautious critics as Seward (1933, p. 110).

Blackwelder (1913) long ago suggested that branched structures in the Ordovician Bighorn Dolomite of Wyoming represent red algae comparable to *Lithophyllum*. So far as is known, these supposed fossils lack microstructure, but that is readily explained by the fact that dolomitic grains in the Bighorn range from .05 to 1.0 mm. in diameter while the cells of modern lithophylloids average .01 in diameter. Moreover, Walther (1919, p. 181) and other authors have emphasized the readiness with which percolating waters destroy the structure of calcareous rhodophytes and even of massive corals.

Undescribed algal structures comparable to those of the Bighorn are abun-

dant in Cambrian formations of southern British Columbia and Alberta, as well as in the Cottonwood district of Utah (Fenton 1943, p. 90; Calkins 1943, p. 15). Others are found in "fucoidal" Ordovician strata of the Mississippi Valley and the East. It seems possible, therefore, that branching rhodophytes which may be compared with the Corallinaceae form a very large part of our early plant record.

Little can be said of the tubular and irregularly expanded structures which are abundant in the Cambrian of the Teton Mountains, and which have been described as *Aulophycus* (Fenton and Fenton 1939, pp. 104-108). Like *Palaeophycus tubularis* of the Trenton (Hall 1847, p. 7), these supposed plants lack microstructure and can be only tentatively referred to the Rhodophyceae.

Most abundant of all fossil algae are the nodular, laminar and vesicular structures known as stromatolites or spongiostromes. Long the subject of debate, these fossils are accepted as algal by a growing number of workers, who include such algologists as Chapman (1941, p. 266), Tilden (1935, p. 5) and apparently Fritsch (1945, p. 859). Following the opinions of Miss Tilden and Wieland (1914, p. 241), Fenton (1943, p. 97) has suggested that many stromatolites were built by aggregations of red algae, with blue-greens playing only a minor role. This opinion is supported by the close resemblance between many stromatolites and the living structures built by known rhodophytes, and is at least consistent with the fact that most stromatolites are found in dolomite or dolomitic limestones. As in the supposed red algae described by Blackwelder, however, such preservation means that there is little chance of finding red algal cells.

As earlier papers have shown (Fenton and Fenton 1937, 1939; Fenton 1943) stromatolites are most satisfactorily interpreted as the product of symbiotic associations consisting of several algal species. These associations produced gross morphologic features of laminae, colonies, columns, etc., which showed remarkable stability in spite of variations to be correlated with the environment. This condition is well shown by *Collenia Willisii* of the Belt, which preserves fundamental characters through strata some 1900 feet in thickness and in sediments which range from fine-grained dolomite to siliceous argillite and edgewise breccias. Such stability seems to indicate a constant group of species whose association was almost as firmly established as that of the alga and fungus which forms a single species of lichen. It also indicates an actual biologic basis for the many species of stromatolites which have been described.

Papers already mentioned have stressed problems to be solved in the study of stromatolites and methods to be employed in securing worth-while collections. These methods call for detached field notes and photographs, with collection of associated sediments as well as stromatolites. Photographs are especially important in dealing with forms so large that whole colonies cannot be collected, or with other forms which show substantial variation. Without photographs, notes and specimens of rock, it is easy for the laboratory worker to misinterpret such stromatolites.

As of today, stromatolites carry the record of algal life back to the Archean Nash Formation of Wyoming, which Blackwelder (letters, 1944, 1946) cor-

relates with formations in the Black Hills, whose age is estimated at 1,465,000,000 years, — apparently late Keewatin. Other stromatolites have been found in latest Keewatin or early Timiskaming (Echo Bay) strata of the Northwest Territories of Canada, whose age is at least 1,200,000,000 years (Fenton and Fenton 1939, p. 91). These early representatives are succeeded by increasingly abundant and varied forms in the Proterozoic and Ozarkian, followed by a rapid decline in Ordovician formations. It is significant, however, that stromatolites did not disappear, for they may be found in Cretaceous and Tertiary formations and in modern seas. They therefore merit careful study in the hope of deriving all possible data from a history which approximates one and one-half billion years.

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Late Paleozoic Algae of North America

J. Harlan Johnson

Paleozoic algae have been mentioned occasionally in geologic literature from the middle of the last century down to the present. However, it is only during the last 15 or 20 years that they have received very much attention. Geologists are just beginning to realize that they occur. Many are still not acquainted with their appearance and ignore them.

There are but few records of finds of Devonian algae. Dawson (1862, 1886) mentioned several Canadian occurrences over 70 years ago, and later writers have mentioned them a few times. However, these early descriptions are so vague and the illustrations so sketchy that it is almost impossible to classify them systematically. Peck (1934) has described a number of fossil *Charophyta*. Beyond that, we have very little information on American Devonian algae. The record is only slightly better for the Mississippian. During recent years, a number of forms have been described from the Pennsylvanian, mainly from Kansas, Oklahoma, Colorado, New Mexico, and Texas. The same is true for the Permian.

In the present paper an endeavor is made to give a brief general review of the late Paleozoic algae, presented systematically according to the character of the algae. The geologic distribution is indicated by charts.

Table 1 presents a key to the groups described. The *Solenoporaceae* have not been recorded from the Devonian of North America, although they are known to occur in rocks of that age in other continents. Several Mississippian species were recently recorded by Johnson (1945) from Colorado. They have been observed in the Pennsylvanian of Kansas, but no forms have yet been described. Pia (1940) and Johnson (1942, p. 200) have described species from the Upper Permian of New Mexico, and Johnson (ms.) has observed several undescribed types from the Permian of West Texas. Future studies will probably uncover and describe many more occurrences of these algae from the Upper Paleozoic, as they seem to be relatively common in Europe.

Several types of algae assumed to belong among the *Phaeophyta* have been described. White (1896) mentioned several from the Mississippian of West Virginia, and some of the frond-like types mentioned by Dawson may belong among the brown algae. Recently Condra and Elias (1944) in their elaborate study of the *Archimedes* have pointed out that the central supporting framework of that "genus" shows a structure very similar to that found in the modern kelp.

The *Chlorophyta* are represented by a number of types. Among the *Charophyta*, five genera represented by a number of species have been described from localities in the United States and Canada. Locally, their remains have

been found in great numbers. It is to be expected that future work will uncover many more.

The *Dasycladaceae* form the most interesting and useable of the fossil green algae. To date seven genera have been recorded from North America—two from the Mississippian, one from the Pennsylvanian, and five from the Permian (see Table 2). In Mississippian beds of Nova Scotia, the remains of the genus *Koninckopora* are locally very abundant and are of interest for their large size, some individuals attaining a length of approximately 50 cm., making them the largest known *Dasycladaceae* (Wood, 1943). Representatives of the genus *Epimastopora* have been found in the Pennsylvanian and Lower Permian at a number of localities in Kansas (Johnson, 1946). In the Upper Permian of southern New Mexico and West Texas, *Dasycladaceae* (particularly members of the genus *Mizzia*) are widespread and locally are so abundant as to be rock-builders (Johnson & Dorr, 1942). Studies in progress indicate the presence of a number of genera and species as yet undescribed. It is interesting to note that the genus *Mizzia* has a world-wide distribution in the Middle and Upper Permian and where found is usually abundant.

Ulke (1938, p. 57) has described a small form from the Mississippian of Indiana to which he applied the generic term *Globulinea*. He classifies them among the Siphoneae.

Members of the *Codiaceae* appear to have had a wide distribution. The genus *Gymnocodium* has been reported from many localities in Europe, Asia, and the East Indies. Recently it has been obtained in West Texas. A closely related genus, *Anchicodium*, is abundant at a number of stratigraphic levels in the Pennsylvanian of Kansas (Johnson, 1946). The genera *Garwoodia* (Mitcheldeania) and *Ortonella* have long been known from the Mississippian of Great Britain. Johnson (1945, p. 839) records their occurrence in the Mississippian of central Colorado. Forms belonging to *Ortonella*, or closely related to it, have been observed in the Upper Permian of West Texas.

Representatives of the *Porostroma* are widely distributed. The genus *Girvanella* occurs in the Mississippian, Pennsylvanian, and Permian and has been reported from Missouri, Nebraska, Kansas, Colorado, New Mexico, and West Texas. The "genus" *Osagia*, originally described from the Permian of northern Oklahoma, occurs abundantly throughout the Lower Permian and much of the Pennsylvanian of Kansas and northern Oklahoma, and recently it has been found in the Ingleside limestone of northern Colorado. The genus *Ottonosia* occurs abundantly in Lower Permian beds of Cowley County, Kansas.

The family *Spongiostroma* was erected by Pia to cover the multitude of forms of low calcareous algae which show little or no microstructure but which develop colonies of constant shape. Such forms are very widespread, although only a few have been described. They seem to have developed commonly in near-shore and brackish water phases of the Pennsylvania and Lower Permian of the Rocky Mountain region, Kansas, Oklahoma, and Texas. Johnson (1940) described a number of Pennsylvanian forms. Fenton and Fenton (1939, p. 113) described a rather spectacular Mississippian form which proba-

bly belongs in this group. Several genera have been described from the Permian of the Carlsbad region (Johnson, 1942, p. 212, 213). Many undescribed occurrences are known in New Mexico and West Texas. Further search will undoubtedly disclose many more.

Harlton (1933) described several problematical forms from the Johns Valley (Pennsylvanian) shale of Oklahoma.

TABLE 1.—Key to Algal Groups Described.

Class	Family	Characteristic Structures
Rhodophyta (Red Algae)	Solenoporaceae	Rows of closely packed cells with polygonal cross sections. Cross partitions present though frequently very thin.
Phaeophyta (Brown Algae)	Laminariales and others (?)	Corded strands of parallel threads (as in framework of *Archimedes* Hall). Fronded types.
Chlorophyta (Green Algae)	Charophyta	Highly developed small bushy plants. Fossils usually consist of calcified heavily ribbed spherical oogonia and the whorled branches which bear them.
	Dasycladaceae	A central stalk, preserved as a tube or bulb, surrounded by tufts of leaves or leaf bases, preserved as knobs or brush-like protuberances.
	Codiaceae	Small tubes loosely arranged so as to form segmented stems. Tubes round in cross section and branching.
Cyanophyta (Possibly Chlorophyta)	Porostromata	Small tubes so loosely arranged as not to compress each other. No cross partitions visible.
Cyanophyta (Blue Green (Algae)	Spongiostroma	Cellular structure seldom preserved. The $CaCO_3$ is deposited as crusts on the outside of the colony or cell, or between the tissues, not in the cell wall. Classified on the basis of growth habit and form of the colony.

TABLE 2.—Upper Paleozoic Algae of North America.

Family	Genus	Age	Geograprical Distribution	Reference
Solenoporaceae	Solenopora	Miss.-Pr.	Colorado, Kansas Texas, New Mexico	Johnson 1945, 1942, 1946
Charophyta	Aclistochara	Pa.-Pr.	Missouri, Kansas	Peck 1937, 1931
	Gyrogotes	Pa.	Missouri	Peck
	Palaeochara	Pa.	Nova Scotia	Bell 1922
	Trochiliscus	Dev.-Miss.	Missouri	Peck
	Sycidium	Miss.	Missouri	Peck
Dasycladaceae	Anthracoporella	Pr.	New Mexico, Texas	Johnson 1942
	Coelosporella	Miss.	Colorado	Johnson 1945
	Diplopora	Pr.	New Mexico	Johnson 1942
	Epimastopora	Pa. & Pr.	Kansas	Johnson 1946
	Koninckopora	Miss.	Nova Scotia	Wood 1943
	Macroporella	Pr.	New Mexico, Texas	Pia 1940, Johnson 1942
	Mizzia	Pr.	New Mexico, Texas	Pia 1940, Johnson & Dorr 1942, Johnson 1942
Codiaceae	Anchicodium	Pa.-Pr.	Kansas	Johnson 1946
	Garwoodia (Mitcheldeania)	Miss.	Colorado	Johnson 1945
	Gymnocodium	Pr.	Texas, New Mexico	Pia 1940, Johnson (ms.)
	Ortonella	Miss.-Pr.	Colorado, Texas	Johnson 1945, Johnson (ms.)
Siphoneae (?)	Globulinea	Miss.	Indiana	Ulke 1938
Porostromata	Girvanella	Miss.-Pr.	Colo., Mo., Kansas	Johnson 1940, 1942, 1945, 1946
	Osagia	Pa.-Pr.	Kansas, Oklahoma	Twenhofel 1919, Johnson 1946
	Ottonosia	Pr.	Kansas, Oklahoma	Twenhofel 1919, Johnson 1946
Spongiostroma	Artophycus	Pa.	Colorado	Johnson 1940
	Calyptophycus	Pa.	Colorado	Johnson 1940
	Collenella	Pr.	New Mexico	Johnson 1942
	Condonophycus	Miss.	Wyoming	Fenton & Fenton 1939
	Cryptozoon	Pa.	Colorado, Kansas	Johnson 1940, 1946
	Gouldina	Pa.	Colorado	Johnson 1940
	Leptophycus	Pa.	Colorado	Johnson 1940
	Shermanophycus	Pa.	Colorado	Johnson 1940
	Stylophycus	Pa.	Colorado	Johnson 1940

TABLE 3.—Devonian Algae.

Family	Genus and Species	Distribution		Reference
		Stratigraphic	Geographic	
Charophyta	Trochiliscus Karpinsky:			
	T. bellatulus Peck	Columbus ls.	Sandusky, Ohio	Peck 1934, p. 115
	T. bilineatus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 113
	T. bilineatus Peck	Snyder Creek shale	Callaway County, Mo.	Peck 1934, p. 113
	T. bilineatus Peck	Columbus ls.	Sandusky, Ohio	Peck 1934, p. 113
	T. devonicus (Wieland) Peck	Jeffersonville ls.	Louisville, Ky.	Peck 1934, p. 108
	T. devonicus (Wieland) Peck	Snyder Creek shale	Callaway County, Mo.	Peck 1934, p. 108
	T. herbertae Peck	Bell shale	Rogers City, Mich.	Peck 1934, p. 115
	T. lemoni (Knowlton)	Jeffersonville ls.	Louisville, Ky.	Peck 1934, p. 106
	T. liratus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 113
	T. liratus Peck	Columbus ls.	Sandusky, Ohio	Peck 1934, p. 113
	T. meeki Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 112
	T. raricostatus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 114
	T. rugulatus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 115

TABLE 4.—Mississippian Algae.

Family	Genus and Species	Distribution		Reference
		Stratigraphic	Geographic	
Solenoporaceae	Solenopora Dybowsky:			
	S. similis Paul	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 837
	S. glenwoodensis Johnson	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson, 1945, pp. 837-838
Charophyta	Sycidium G. Sandberger:			
	S. clathratum Peck	*Sylamore fm.*	Williamsburg, Mo.	Peck 1934, p. 117-118
	S. foveatum Peck	*Sylamore fm.*	Williamsburg, Mo.	Peck 1934, p. 117
	Trochiliscus Karpinsky:			
	T. decacostatus Peck	*Sylamore fm.*	Williamsburg, Mo.	Peck 1934, p. 109
	T. laticostatus Peck	*Sylamore fm.*	Williamsburg, Mo.	Peck 1934, p. 109
	T. octocostatus Peck	*Sylamore fm.*	Williamsburg, Mo.	Peck 1934, p. 111
	T. septemcostatus Peck	*Sylamore fm.*	Williamsburg, Mo.	Peck 1934, p. 111
Dasycladaceae	Coelosporella Wood:			
	C. sp.	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 838
	Koninckopora Lee:			
	K. inflata (de Koninck)	Middle Winsor ls.	Point Edward, Nova Scotia	Wood 1941, p. 211
Codiaceae	Garwoodia (Mitcheldeania):			
	G. aff. gregoria (Nicholson)	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 839
	G. media Johnson	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 839
	Ortonella Garwood:			
	O. furcata Garwood	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 839
	O. cf. *kershopensis* Garwood	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 839
	O. coloradoensis Johnson	Upper Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 840
Siphoneae (?)	Globulineae Ulke:			
	G. giganteus Ulke	Salem ls.	Indiana	Ulke 1938, p. 58
Porostromata	Girvanella Nicholson & Etheridge:			
	G. maplewoodensis Johnson	Ste. Genevieve	St. Louis, Mo.	Johnson 1946, p.
	G. ? *nicholsoni* (Wethered)	Leadville ls.	Glenwood Springs, Colo.	Johnson 1945, p. 840
Spongiostroma	Condonophycus Fenton & Fenton:			
	C. austinii Fenton & Fenton	Madison ls.	Big Horn Mts., Wyo.	Fenton & Fenton 1939, p.113
Charophyta	Trochiliscus Karpinsky:			
	T. bellatulus Peck	Columbus ls.	Sandusky, Ohio	Peck 1934, p. 115
	T. bilineatus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 113
	T. bilineatus Peck	Snyder Creek shale	Callaway County, Mo.	Peck 1934, p. 113
	T. bilineatus Peck	Columbus ls.	Sandusky, Ohio	Peck 1934, p. 113
	T. devonicus (Wieland) Peck	Jeffersonville ls.	Louisville, Ky.	Peck 1934, p. 108
	T. devonicus (Wieland) Peck	Snyder Creek shale	Callaway County, Mo.	Peck 1934, p. 108
	T. herbertae Peck	Bell shale	Rogers City, Mich.	Peck 1934, p .115
	T. lemoni (Knowlton)	Jeffersonville ls.	Louisville, Ky.	Peck 1934, p. 106
	T. liratus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 113
	T. liratus Peck	Columbus ls.	Sandusky, Ohio	Peck 1934, p. 113
	T. meeki Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 112
	T. raricostatus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 114
	T. rugulatus Peck	Hackberry fm.	Rockford, Iowa	Peck 1934, p. 115

TABLE 5.—Pennsylvanian Algae.

Family	Genus and Species	Distribution		Reference
		Stratigraphic	Geographic	
Solenoporaceae	Solenopora Dybowsky:			
	S. sp. ?	Pennsylvanian	Kansas	Johnson ms. 1946
Charophyta	Aclistochara Peck:			
	A. moreyi Peck	Cherokee fm.	Mo. & Kans.	Peck, 1937, p. 86
	Gyrogonites Lamarck (?):	Cherokee fm.	Missouri	Pia 1937, p. 812
	G. robertsi Peck	Cherokee fm.	Columbia, Mo.	Peck 1934, p. 54
	Paleochara Bell:			
	P. acadica Bell	Pennsylvanian	Nova Scotia	Bell 1922, p. 160
Dasycladaceae	Epimastopora Pia:			
	E. (4 species) Johnson	Middle & Upper	Kansas	Johnson ms. 1946
Codiaceae	Anchicodium Johnson (ms.)	Middle & Upper	Kansas	Johnson ms. 1946
Porostroma	Girvanella N. & E.:			
	G. (3 sp.) Johnson	Middle & Upper	Kansas	Johnson ms. 1946
	G. sp. Johnson	Weber shale	Colorado	Johnson 1940, p. 591
	Osagia Twenhofel	Middle & Upper	Kansas	Johnson ms. 1946
Spongiostroma	Artophycus Johnson:			
	A. columnaris Johnson	Weber shale	Colorado	Jonhson 1940, p. 589
	Calyptophycus Johnson:			
	C. verructus Johnson	Webes shale	Colorado	Johnson 1940, p. 590
	Cryptozoon Hall:			
	C. coloradoensis Johnson	Weber shale	Colorado	Johnson 1940, p. 590
	C. (2 sp.) Johnson	M. & U. Pa.	Kansas	Johnson ms. 1946
	Gouldina Johnson:			
	G. carbonaria Johnson	Weber shale	Colorado	Johnson 1940, p. 583
	G. magna Johnson	Weber shale	Colorado	Johnson 1940, p. 585
	Leptophycus Johnson:			
	L. gracilis Johnson	Weber shale	Colorado	Johnson 1940, p. 586
	Shermanophycus Johnson:			
	S. gouldi Johnson	Weber shale	Colorado	Johnson 1940, p. 582
	Stylophycus Johnson:			
	S. carbonarius Johnson	Weber shale	Colorado	Johnson 1940, p. 587
	S. calcarius Johnson	Weber shale	Colorado	Johnson 1940, p. 588
	S. radiatus Johnson	Weber shale	Colorado	Johnson 1940, p. 589

TABLE 6.—Permian Algae.

Family	Genus and Species	Distribution		Reference
		Stratigraphic	Geographic	
Solenoporaceae	Solenopora Dybowsky:			
	S. centurionis Pia	Capitan ls.	New Mexico	Pia 1940, p. 3 Johnson 1942, p. 200
	S. sp. ind. Pia	Capitan ls.	New Mexico	Pia 1940, p. 3
	S. sp. Johnson	Capitan ls.	New Mexico	Johnson 1942, p. 201
Dasycladaceae	Anthracoporella Pia:			
	A. sp. Johnson	Capitan ls.	New Mexico	Johnson 1942, p. 209
	Diplopora Schafhäutl:			
	D. sp. ? Johnson	Capitan ls.	New Mexico	Johnson 1942, p. 209
	Epimastopora Pia:			
	E. (1 sp.) Johnson	Foraker ls.	Kansas	Johnson 1946 (ms.)
	Macroporella Pia:			
	M. verticillata Pia	Capitan ls.	New Mexico	Pia 1940, p. 2
	M. cf. *verticillata* Johnson	Capitan ls.	New Mexico	Johnson 1942, p. 208
	Mizzia Schubert:	Capitan ls.	New Mexico	Pia 1940, p. 2
	M. velebitana Schubert	Capitan ls.	Texas (Apache Mts.)	Johnson & Dorr 1942, p. 71
	M. velebitana Schubert	Capitan ls.	N. Mex. & Tex.	Johnson 1942, p. 203
	M. velebitana Schubert	Capitan ls.	N. Mex. & Tex.	Johnson & Dorr 1942, p. 73;
	M. minuta Johnson & Dorr	Capitan ls.	N. Mex. & Tex.	Johnson 1942, p. 205
	M. Yabei (Karpinsky)	Capitan ls.		Johnson & Dorr, p. 75 Johnson 1942, p. 207
Codiaceae	Anchicodium Johnson:			
	A. permianum Johnson (ms.)	Foraker ls.	Marshall Co., Kans.	Johnson (ms.) 1946
	Gymnocodium Pia:			
	G. sp. Pia	Capitan ls.	New Mexico	Pia 1940, p. 3
	G. 2 sp. undes.	Capitan ls.	Texas	Johnson (unpublished)
Porsotromata	Girvanella N. & E.:			
	G. (2 sp.)	L. Permian	Kansas	Johnson ms. 1946
	G. sp. Johnson	Capitan ls.	New Mexico	Johnson 1942, p. 211
	Osagia Twenhofel	Foraker to Ft. Riley		
	Ottonosia Twenhofel	Foraker ls.	Kansas	Johnson ms. 1946
	O. laminata	Foraker ls.	Cowley Co., Kansas	Twenhofel 1919, p. 348 Twenhofel 1919, p. 350
	Collenella Johnson:			
	C. guadalupensis Johnson	Capitan ls.	Carlsbad N. Mex.	Johnson 1942, p. 212

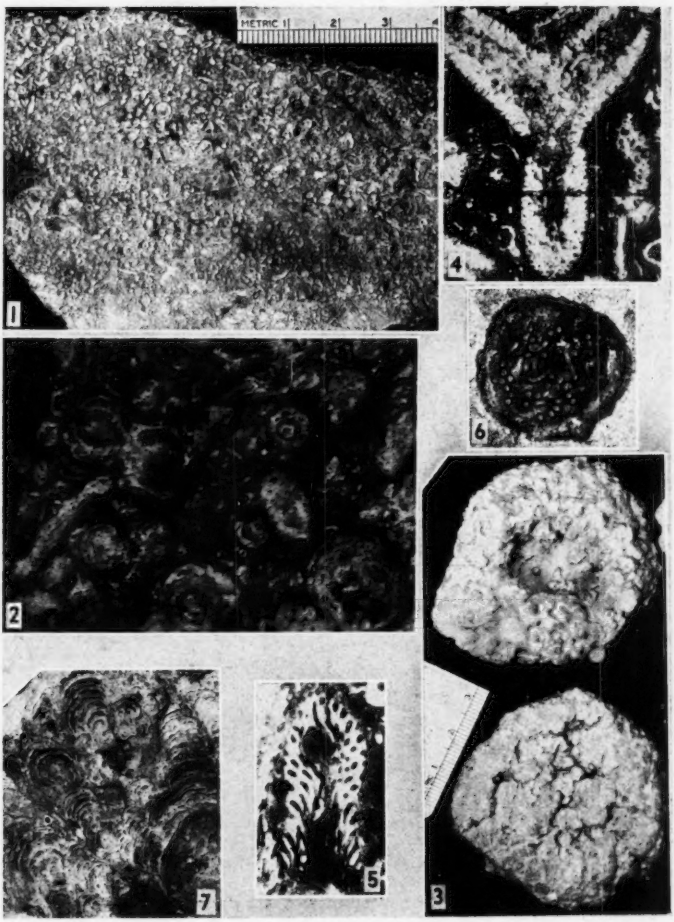

PLATE 1.—1. *Mizzia* Limestone. Permian; Apache Mountains, Texas. Composed largely of *Mizzia velebitana*. 2. Detail of above (×12). 3. *Ottonosia laminata;* Permian; Cruse limestone; Cowley County, Kansas. 4. *Gymnocodium bellerophontis;* Permian, Europe (Tyrol). (×20); after Pia 1937. (Scale slightly smaller than indicated.)

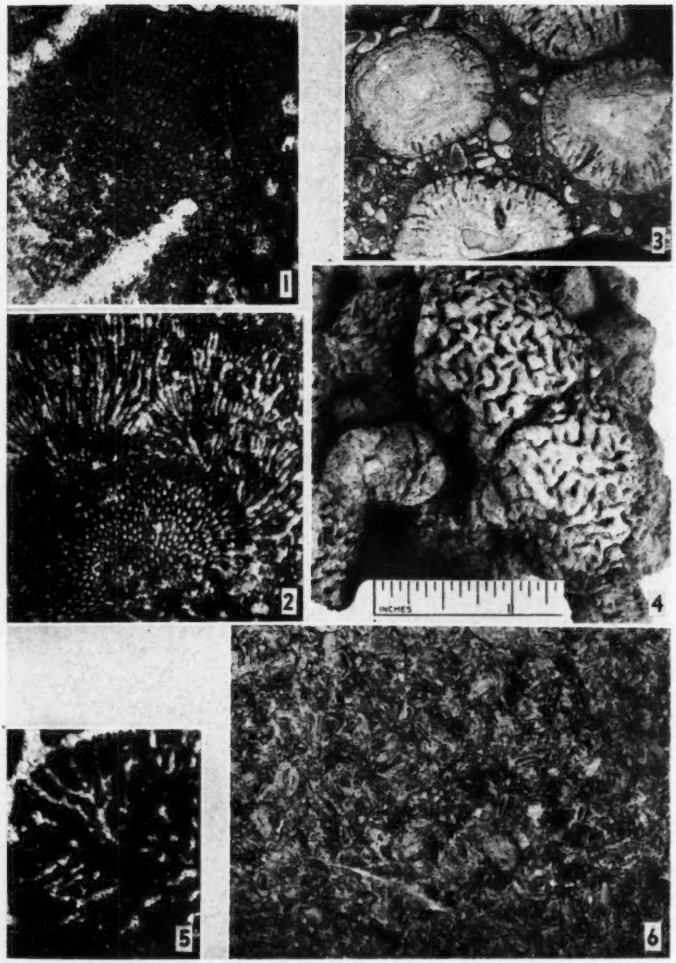

PLATE 2.—1. *Solenopora glenwoodensis* (×25); Mississippian Leadville limestone, Glenwood Springs, Colorado. 2. *Garwoodia* aff. *gregaria* (×14); Mississippian Leadville limestone, Glenwood Springs, Colorado. 3. *Somphospongia multiformis* (×2/3); Pennsylvanian Burlingame limestone, Brown County, Kansas. A natural eroded cross section. 4. Same a specimen showing surface appearance. 5. *Ortonella furcata* (×40); Mississippian Leadville limestone, Glenwood Springs, Colorado. 6. Osagia limestone, composed largely of *Osagia* cf. *incrustata* (×1½); Pennsylvanian, Upper Hertha limestone, Linn County, Kansas. (Scale slightly smaller than indicated.)

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COLORADO SCHOOL OF MINES,
GOLDEN, COLORADO.

Fossil Charophyta

Raymond E. Peck

Charophyta constitute a small group of fresh and brackish water plants of somewhat doubtful affinities. Some systematists rank them as a class of the Thallophyta and others group them as a separate phylum. They occur abundantly in quiet bodies of clear water such as ponds, ditches, gravel pits, or lakes, and are widely distributed throughout the world. Occasionally they are found in rivers or in brackish water. Because they live completely covered by water they are inconspicuous and have attracted little attention. They are of interest to the geologist as stratigraphic fossils and because some species secrete calcium carbonate and are large contributors to fresh water limestones. They are of interest to the botanist because of the uncertainty of their systematic position.

The antheridia and oogonia of charophytes are very complex and highly organized bodies, entirely unlike those of any other plant, and it is because of them that the systematic position of the Charophyta is so uncertain. These bodies develop at the nodes of the branchlets and stalk.

The antheridia are subspherical in shape, and one mm. or less in diameter. The outer wall is made up of eight convex plates essentially triangular in outline. These plates are grooved on the outside and the edges are irregularly crenulate. The antheridia do not calcify on modern charophytes and have been recognized in the fossil state only in the Upper Jurassic of England and the Lower Cretaceous of North America.

The oogonia are subspherical in shape and some attain a maximum of one and a half millimeters in diameter. The outer wall is composed of five or more elongated enveloping cells that spiral either to the right or to the left. In Mesosoic, Cenozoic, and modern charophytes the spiral is always to the left. Situated on the terminal ends of these five cells are one or two circlets of five small cells, forming the coronula.

Charophyte oogonia may be preserved as fossils by virtue of their ability to secrete fine-grained calcium carbonate. This deposition starts on the concave inner walls of the enveloping cells and may almost completely replace the cell contents. Coronula cells do not calcify on modern charophytes but did calcify and are preserved on some fossil oogonia.

Charophyta are represented in the fossil state primarily by oogonia. Broken and fragmentary vegetative parts have been discovered and described, and on one species in the Purbeck of England the antheridia are preserved. Most genera and species are based on oogonia.

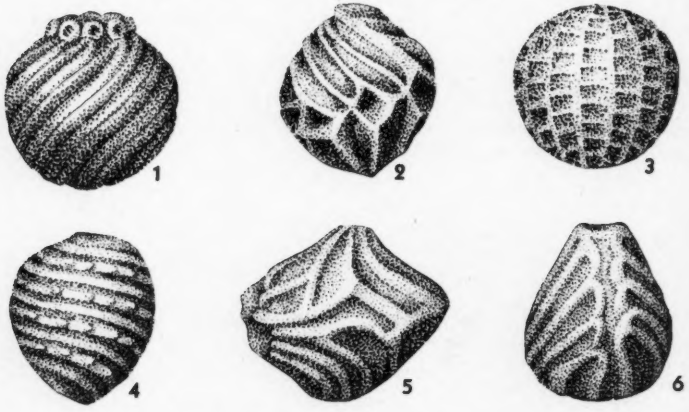
Fossil charophytes are most easily and successfully obtained from fresh-water calcareous shales. In practice, an attempt is made to find a fresh-water

limestone or a limestone in what is generally accepted as a fresh-water formation. A sample is gathered from shale partings within the limestone or from shale immediately under or over the limestone. Generally about a quart of shale is collected but the amount depends on the accessibility of the material. The sample is then taken into the laboratory, water is added and the sample is boiled. Boiling breaks down the coherence of the material and brings the clays into suspension. Frequent but careful flushing removes the clays and leaves a clean residue. This residue is dried and the charophyte oogonia are selected under a binocular microscope with a moistened brush.

The oogonia often occur in limestone from which free specimens may be obtained by crushing. In a few occurrences the fossils are silicified and may be removed by dissolving the limestone matrix in acid.

Fossil charophytes may be grouped into four families, the Characeae, the Clavatoraceae, the Trochilischaceae, and the Sycidiaceae. The Characeae comprise the modern type of charophytes and range from Cherokee (the Pennsylvanian) to the present. The Clavatoraceae are confined to the uppermost Jurassic and Lower Cretaceous periods. The Trochiliscaceae and the Sycidiaceae are confined to pre-Pennsylvanian sediments.

Oogonia of the Characeae always have five sinistrally spiralled enveloping cells (Fig. 4). The oldest known occurrence of an oogonium of this type is from the Cherokee (Pennsylvanian) sediments of Missouri. They occur sparsely in Pennsylvanian, Permian, and Triassic sediments and are quite common in the Morrison (Jurassic) and younger fresh-water sedimentary rocks. For the most part, these oogonia are less than one millimeter in diam-



EXPLANATION OF FIGURES

Fig. 1. *Trochiliscus octocostatus* Peck. Fig. 2. *Atopochara trivolvis* Peck. Fig. 3. *Sycidium foveatum* Peck. Fig. 4. *Aclistochara* sp. Fig. 5. *Permineste corrugata* Peck. Fig. 6. *Clavator harrisi* Peck.

eter, slightly higher than broad, and difficult to differentiate into genera and species. Surface ornamentation depends largely on the amount of calcite secreted within the enveloping cells and this may vary markedly on oogonia from the same plant.

Two exceptions from this standard type have been recorded. *Paleochara acadica* Bell (1922) from the Pennsylvanian of Nova Scotia possesses six sinistrally spiralled cells instead of five, but this genus is apparently restricted geographically. Starting in uppermost Cretaceous and continuing through early Tertiary large (maximum 1.4 mm. diameter) spherical oogonia on which coronula cells calcified are found. On many of these large oogonia prominent nodes were developed on the enveloping cells (Kosmogyra Stache). These oogonia are very abundant in the early Tertiary of India, Italy, France, England, Peru, Florida, and the northern Rocky Mountain region, and are sufficiently distinctive to be used as stratigraphic markers.

The Clavatoraceae comprise a peculiar group of fossil charophytes that secreted a utricle or nut covering over the oogonia. This utricle calcified and has a distinctive and complicated surface ornamentation. It adheres closely to the calcified oogonia within but is found in all degrees of exfoliation. Three genera of this family have been described. The genera *Clavator* (Fig. 6) and *Permineste* (Fig. 5) were described from the Purbeck of England and were recently monographed by Harris (1939). The genus *Atopochara* (Fig. 2) was described from the Lower Cretaceous of Texas and apparently is confined to the North American continent. In his work on the Purbeck, Harris was able to associate vegetative parts with reproductive organs and describe *Clavator* and *Permineste* in great detail. *Atopochara* is represented only by oogonia. Oogonia of *Atopochara* and *Clavator* and antheridia of *Permineste* are widely distributed and abundant in the Lower Cretaceous of the Gulf and northern Rocky Mountain regions of the United States (Peck, 1941). *Permineste* is unique in that it is the only representative of fossil charophytes on which the antheridia are calcified and preserved.

The Trochiliscaceae (Fig.) comprise a group of oogonia with from seven to ten dextrally spiralled enveloping cells and with or without calcified coronula cells. This family is confined to the Devonian and lower Mississippian periods and is widely distributed in North America and Europe. This group was first described by Pander in 1856 from the Devonian of Russia and has since been studied comprehensively by Karpinsky (1906) and Peck (1934).

The Sycidiaceae (Fig.) are characterized by possessing a calcareous oogonium composed of from sixteen to twenty vertical units. These units are divided horizontally so as to give an oogonium with a variable number of pits and nodes, according to the degree of calcification. The Sycidiaceae are more common in the Devonian of Europe than the Trochiliscaceae but in North America are known from only one locality in one formation. The genus Sycidium was first recorded by G. Sandberger in 1849 from the Devonian of Eifel but has since been comprehensively treated by Karpinsky (1906) and Peck (1934).

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Algae as Ecologic Indicators

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Fossil algae, somewhat neglected in the past because of difficulties of identification, have come in for an increasing amount of attention during recent years. If identifiable, they can add their bit of evidence to the general habitat, or paleoecological picture.

Paleoecology, on the whole, draws its evidence from plants, animals, and sediments which, to a greater or less extent, reveal information on the conditions surrounding them during life or, in the case of sediments, during formation. In somewhat different words, paleoecology depends upon coordinated evidence among plants, animals, and sediments, and includes a study of all interacting, inter-related factors that influence or leave an impress upon organisms or the sediments in which they were entombed.

Plants and animals during life are subject to environmental influences, both organic and inorganic, some so restrictive as to determine limitations of dispersal. In the case of plants, a paleoecological analysis may be built upon a combination of present distribution of related forms (within limits), internal anatomy, floral assemblages, and enclosing sediments. The first two are concerned strictly with the habitat, or even micro-habitat, in which the plants lived; the second two may be modified by transportation, by the environment during transportation and at the site of deposition. Therefore, plants should be studied not simply as plants or assemblages of plants but also as component parts of the sediments enclosing them.

A complete outline of factors relative to the paleoecology of fossil algae, within small compass, would be merely a feeble attempt to express the principles of paleoecology. Only a few points can be emphasized here for the purposes of suggestion.

Present-day distribution of the algae considered alone can be of highest significance or can have little or no significance whatsoever. For instance, the Blue-Green Algae are nearly ubiquitous over land and water; they are terrestrial and marine. They endure temperature extremes from the lakes of Alaska to hot springs well over 100 degrees F. Taken alone Blue-Green Algae are apparently unsatisfactory as temperature indicators. Their value, if any, must be gained elsewhere.

Rhabdospheres and Coccospheres, grouped under the Coccolithophoridae, are commonly considered to be algae. For one reason or another little study has been given these small forms. They abound in the surface waters of the oceans. Some of them are restricted to tropical waters, others range from the Tropics into the Temperate Zones. As rock-makers they well deserve detailed studies occurring as they do so abundantly in the Mesozoic and known back into the early Paleozoic.

The Brown Algae, in general, characterize the cold waters of high latitudes and with few exceptions they are Arctic and sub-Arctic. In addition, their development becomes increasingly greater away from the warmer waters, so

much so that they are poorly represented in the Tropics and are predominant in the Arctic. It is apparent, therefore, that the Brown Algae, if identifiable, can be of considerable importance in Paleoecology.

Green Algae are widespread over the surface of the earth, although they are on the whole fewer and more poorly developed in cold than in warm waters. Nearly all the forms represented in fossil records belong to the Siphoneae which today live almost wholly in tropical and subtropical seas. The Green Algae are important in geologic records as fossil forms, as rock-makers, and as ecologic indicators.

Even though Red Algae have been found in all latitudes up to and beyond the Arctic Circle they typify more especially temperate and tropical waters where, in the latter place, they are most prolifically represented. Those forms represented in the geologic record are likewise widespread in latitude. However, they perform their function as rock-makers and rock-binders best in tropical waters.

The above gives a few suggestions on present distribution of algae based upon systematic determinations alone. Surely the present distribution of algae has some ecologic information of value to the ecologic interpretation of fossil representatives. When, however, systematic determinations are combined with an analysis of sediments, fossil algae can make definite contributions to paleoecology. This is especially true of the calcareous algae. Blue-Green Algae taken alone, as before mentioned, have little if any ecologic value. Their contributions to thick calcareous deposits do have significance because abundant calcium carbonate accumulating without re-solution requires special conditions.

Because the Brown Algae have no important lime-secreting forms and contribute little to rock making they must be interpreted on a systematic basis, if at all. The algal flora of the European Flysch Formation, if correctly identified as Brown Algae, would suggest ecologic conditions similar to those under which like forms thrive today. Furthermore, the physical conditions during Flysch time do not seem incompatible with such suggested conditions.

The Green Algae as a whole are cosmopolitan but those common to the fossil record and those secreting calcium carbonate abundantly inhabit tropical and subtropical seas today. Here, under the Siphoneae, come such genera as *Penicillus, Halimeda,* and *Cymopolia* whose geological counterparts have been found in extensive formations as far back as the Ordovician.

Red Algae resemble the Green in their general distribution, although they are more characteristic of temperate and tropical regions. Even the lime-secreting forms are rather widespread. It is questionable, however, if considerable amounts of limestone can accumulate in cold waters. In spite of the fact that *Lithothamnion,* one of the most important corallines, precipitates calcium carbonate in Arctic regions where it adds a calcareous component to muds and other clastics or intercalated crusts of limestones, it makes its chief contribution to rock strata in warm waters. This is no doubt true because temperature aids precipitation of calcium carbonate, because algal life is abundant, and because the water is more nearly saturated with calcium carbonate than in colder regions. In fact, the family to which *Lithothamnion* belongs has been credited in many cases with contributing more toward reef construction than any other type of organism. The Calcareous Algae, on the whole, seem to

flourish and do their most important work in water clear, shallow, and warm.

The purpose here has been to give only a few hints on how algae may be used to indicate something about ecologic conditions. The history of plant life on the earth, one ventures to say, is more than systematic descriptions, more than a chronicle of differentiation and evolution. It is also a determination and interpretation of those conditions under which the plants have lived and died. Systematic descriptions are preliminary but highly invaluable requisites for ecologic studies. In other words, specific, anatomical, floristic, and sedimentary evidence may well be combined into a picture including not only the plants themselves but also the environmental details as a colorful background to them. Paleoecology has become to an increasing number of workers the ultimate and fascinating goal. With respect to the higher plants, the work of E. W. Berry and that of R. W. Chaney and his students stand out as distinct contributions to earth history. Cannot the Algae, in their own way, make a like contribution?

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Fossil Symbiotic Algae in Comparison with Other Fossil and Living Algae

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The science of fossil algae or paleophycology has been developing at a somewhat slower rate than most of the other branches of paleontology. Identifications of algae in various states of fossilization, and, especially, their classification with the living algal phyla by paleobotanists were frequently severely criticized by phycologists. While this criticism, was, at times, so severe as to border on discouragement, it served, on the other hand, a useful purpose in making paleontologists conscious of the complexities involved even in the study of the living algae and their taxonomy, and it cautioned them to a more reserved and discriminate attitude in regard to determination and classification of fossil marine plants. Modern critical analysis of the systematic standing of many "fossil algae" described in the early papers by Hall, Walcott, and others showed how questionable is their reference to algae, and especially to definite algal phyla, and it is now realized that even some of the finest recent microscopic work on fossil algae, such as that by Reis (1923) and Bradley (1929), did not solve unequivocally the problem of their relationship with particular living algae (see the criticism by Fritsch 1935, p. 12). Fritsch demonstrates that some fundamentally similar types of somatic organization developed independently in more than one order of living algae, and therefore, the morphology of simply organized fossil algae generally cannot be used, without additional evidence, in an attempt to trace their phyletic relationships. One of the additional critical characters would be pigment, so widely used in the principal division of the living algae—but this evidence is lacking in the fossil material. Another would be types of fructification—but these too are absent in the great majority of fossil algae. Of other criteria for precise identification there remain only detailed anatomical structure, which is seldom observable, and a combination of various morphological features in a complex algal soma which may provide reasonable evidence for a natural classification of fossil algae.

The fossils which have been classified as algae with a varying degree of probability may be conveniently grouped, for the sake of the following brief discussion, in four major categories:

(1) Highly symmetrical, small growth-forms.
(2) Carbonaceous compressions, pseudomorphs, and impressions.
(3) Calcareous precipitations of mixed algal and non-algal nature.
(4) Prostrate, crust-like, and ramose, purely algal or predominantly algal growth-forms.

In the first group belong the forms which bear a striking morphological and anatomical resemblance to those attractive living algae, which are well known for their beautiful geometrical symmetry, and the taxonomy of which

is well established. Such are the microscopic, richly ornamented diatoms, the highly symmetrical and complex Dasycladaceae, and the unique *Chara* and its kin, with spirally ornamented oogonia. Good examples of the recent work in America on these complex, fancifully ornamented and symmetrical algae may be found in the papers by Raymond Peck (on Charophyta) and J. Harlan Johnson (on Dasycladaceae).

These most reliably identified algae of group No. 1, as we may call it, are largely unfamiliar to most field geologists who habitually collect fossils; quite different fossils became popularly known to them as "algae." These are as follows:

Group No. 2 which consists of carbonaceous compressions of algal-like thalli, and their various pseudomorphs and impressions, which bear general resemblance to some living leathery algae, but the true affinity of which is very difficult to prove.

The common kidney- and cauliflower-shaped encrustations and lumps, which seldom possess traces of organic structure, comprise group No. 3. For these forms, Pia erected the artificial group-name *Spongiostromata*, with two subdivisions: Stromatolithi and Oncolithi, and summarily referred them to Blue-Green Algae (Schizophyceae). Many generic names were introduced for these fossil forms, the most commonly used by American geologists being *Cryptozoon* Hall, *Collenia* Walcott, *Osagia* Twenhofel, and others. It is important to realize that, in contradistinction to the first discussed group of reliably identified fossil algae, these fossil lumps and incrustations of group 3 do not correspond to actual somata of living algae, but are merely accumulations of successive calcareous precipitations, presumably by the countless film-like aggregates of microscopic simple colonial algae, and are mixed with calcium carbonate precipitated by organisms other than algae, or (and) precipitated inorganically. Perhaps the most important paper on similar modern aggregate-forms, which involve some living blue green algae, is that by Black (1933). He demonstrates how various types of what may be called living Stromatolithi are now being formed off the shore and in lagoons of the Bahama islands. Black discusses convincingly the control of their "morphologic" features by the environment and sedimentation, the gelatinous algae merely cementing and giving a peculiar kidney-like structure to sand and mud.

In group No. 4, may be placed the various fossils which have a clearly recognizable algal anatomy, but a less clearly recognizable morphology. Their tissue is composed of variously oriented threads of filaments, or is of complex cellular structure, both resembling the tissues of various living calcareous algae. In this group may be placed the fossil lumps, ramified somata, and encrustations, some of which are externally similar to the smaller forms of Stromatolithi and Oncolithi. However, both the external morphological and internal anatomical features in these fossils are not the result of cumulative precipitation of calcium carbonate by successive generations of film-like aggregates of simple algae, mixed with precipitations by various other organic and inorganic agencies, but actually belong to algal somata or to aggregates of somata. In this group belong the living and fossil genera *Lithothamnium, Archaeolithothamnium, Girvanella, Ortonella, Garwoodia, Mitcheldeania* (of authors)

Solenopora, Prototaxites (if an alga), and others. Although these fossils are now frequently placed in definite classes and even families of living Algae (see Pia, 1927; Paul, 1939), the taxonomic position of some of them is still open to dispute, and a few were at various times removed from algae and compared with Gymnosperms (*Prototaxites*) and with *Stromatoporoidea* (*Solenopora* and others). Excellent work has been done on Mesozoic and Cenozoic Corallinaceae by Howe, Lemoine, Rothpletz, Trauth, Pčelincev, Martelli, and others, and comparison of these with living algae has been placed on a sound biological basis. If taxonomic treatment of genera and species within this group is difficult, this is only natural because the living encrusting Melobesieae are protean forms, difficult to classify; and the fossil ones are even more so, because of the poor preservation of fruiting structures in them. The difficulty in the study of Paleozoic fossils which are believed to belong to the same group and are classified as Solenoporaceae (Pia, 1927), is augmented by less perfect preservation, and by the extremely rare and doubtful occurrence of organs of reproduction in them.

Only very few families of living algae have been proved by their fossil remains to have existed in the Paleozoic, and it is curious that the only reasonably biologically identified paleozoic algae belong to the most highly organized among the living Green Algae: Dasycladaceae and Charophyceae; likewise, the above mentioned but somewhat less certainly identified Paleozoic red algae are comparable in complexity to rather well advanced encrusting Melobesieae, —Paleozoic *Solenopora;* and the Paleozoic brown algae, if correctly classified, are also represented by a type (*Prototaxites*), whose extraordinary (for an alga) size and highly advanced woodlike structure are so puzzling, that it was originally referred to primitive conifers (hence the misleading generic name), and whose general systematic position in the Plant Kingdom is still under serious dispute (Lang, 1937). On the other hand, to algae are referred a great many gregarious, minute and very simply organized filamentous fossil forms (*Girvanella* and others), and, though their systematic standing even among the classes of living algae is very difficult to prove, their general algal nature is determined beyond reasonable doubt.

Thus, as far as the present fossil record, especially from the Paleozoic, is concerned, there is no direct evidence at hand to indicate in what manner the very simple filamentous forms evolved into more advanced living algae. It is natural, therefore, that the only attempts to attack this crucial problem in algal evolution have been based entirely on comparative studies of the somatic organization and ontogeny of living algae.

The major problem of paleophycology is, therefore, to find some anatomically well preserved fossil forms that might fill the existing phyletic gap, and demonstrate by their microstructure some intermediate steps in the evolution from simple isolated filaments to more compact and solid somata, which are so well represented in the almost infinite variety of the most wonderfully diversified forms among the living green, brown, and red algae. Perhaps the peculiar plant-like encrustations and "appendages," which are so common on paleozoic bryozoa, and are now called phytomorphs (Condra and Elias, 1942) and are being studied in detail (Elias), represent a part of the missing record of evolution from filamentous to pseudoparenchymatous (Fritsch) or even true paren-

chymatous stages, which are so characteristic of the higher marine algae. Following is a brief account of morphology and anatomy of phytomorphs, which appear to be algae in symbiotic growth with fenestrate bryozoa.

In 1869, P. Martin Duncan and H. M. Jenkins described under the name *Palaeocoryne* what they believed to be a tubularian hydrozoan attached to *Fenestella*, a common fenestrate bryozoan, in the shale of the lower Carboniferous (=Mississippian) of Ayrshire and Lanarkshire of England. Prior to their interpretation Lonsdale expressed a thought that a coral-like form encrusts upon some paleozoic bryozoa. Duncan and Jenkins' conclusion was promptly challenged by a specialist on living hydrozoa, G. J. Allman (1872) of Scotland, who suggested that *Palaeocoryne* could be rather a rhizopod; but this opinion, in turn, was rejected by Duncan, as well as other naturalists who joined in the dispute. Young and Young (1874) of England rejected any possibility that *Palaeocoryne* and similar appendages on *Fenestella* could be a parasitic animal on this bryozoan, and concluded that these appendages are developed by the bryozoan colonies themselves, even though they admitted absence of similar structures on the known living bryozoa, and found it difficult to explain their possible meaning. Vine (1879) suggested that they could have served propagative functions, but found no support for this opinion among other naturalists. Most paleontologists in England and America (Nicholson and Lydekker, 1889; Nickles and Bassler, 1900) agreed with Young and Young in that all the discussed appendages and encrustations on *Fenestella* and other paleozoic bryozoa are part of their colonies, and thus the controversy seemingly was brought to an end. However, the questions about the nature and function of the appendages were left unanswered, and some naturalists continued to believe that they represent remains of some invertebrates parasitic on the bryozoa.

The encrusting tissue on some paleozoic bryozoa came to my attention in 1939, when working jointly with Dr. Condra on American late Paleozoic bryozoa. One of the largest and most interesting of the American fossil genera, the screw-like *Archimedes*, is heavily encrusted and frequently adorned with appendages, and proved to be good material for the study of the controversial problem in regard to the nature of the encrustations and the appendages on the late Paleozoic bryozoa. The following features in the encrusting tissue of *Archimedes* seem indicative of its algal rather than animal nature:

1. The tissue is composed of fine, closely packed fibers.

2. At some points individual fibers bifurcate.

3. On very few specimens of some species there is a sporadic development along fibers of numerous globular bodies, which resemble unilocular sporangia in certain simpler filamentous algae.

4. The tissue shows distinct evidence of originally having been soft and plastic, but subsequently having become calcified.

5. The fibers are arranged in vertical rows radiating from the axis of a screw. In addition, the whole structure is twisted around the axis.

6. In some screws there is a distinct concentric zoning of the radiating tissue, similar to concentric rings observed in older stipes of living *Laminaria*.

7. The diameter of fibers is of same magnitude as in *Laminaria* and other brown and red algae.

8. The fibers are occasionally transversely differentiated into numerous equal to subequal short cells, similar to differentiation of the filaments in living algae.

9. The whole of the phytomorph in *Archimedes,* when completely preserved, shows differentiation into parts comparable to holdfasts, stipes and extensive laminae of the living brown algae. The living *Thalassiophyllum* is nearest to *Archimedes,* minus the bryozoan symbiont and calcification.

Abundant and well preserved material of fossil *Palaeocoryne,* which was the subject of a lively controversy in England some 75 years ago, is now for the first time being recognized and collected in the rocks of Mississippian age in Utah, Illinois and Montana. The American *Paleocoryne,* just as its original types from England, is invariably attached to the obverse or the face side of the bryozoan *Fenestella,* and spreads its tentacle-like branches (somewhat comparable to the tentacles of some Hydrozoa) in umbrella-like fashion just above the rows of polypides of the colony, as if it were catching its nourishment from the water currents sucked in and expelled by the polypides. The finely serrated and hook-bearing branches of some species of *Palaeocoryne* and that belonging to an unnamed new genus are much like the hooked branches of the living *Asparagopsis armatus,* a common sea-weed of the shores of Australia, which became common also in the Mediterranean and in the bays of

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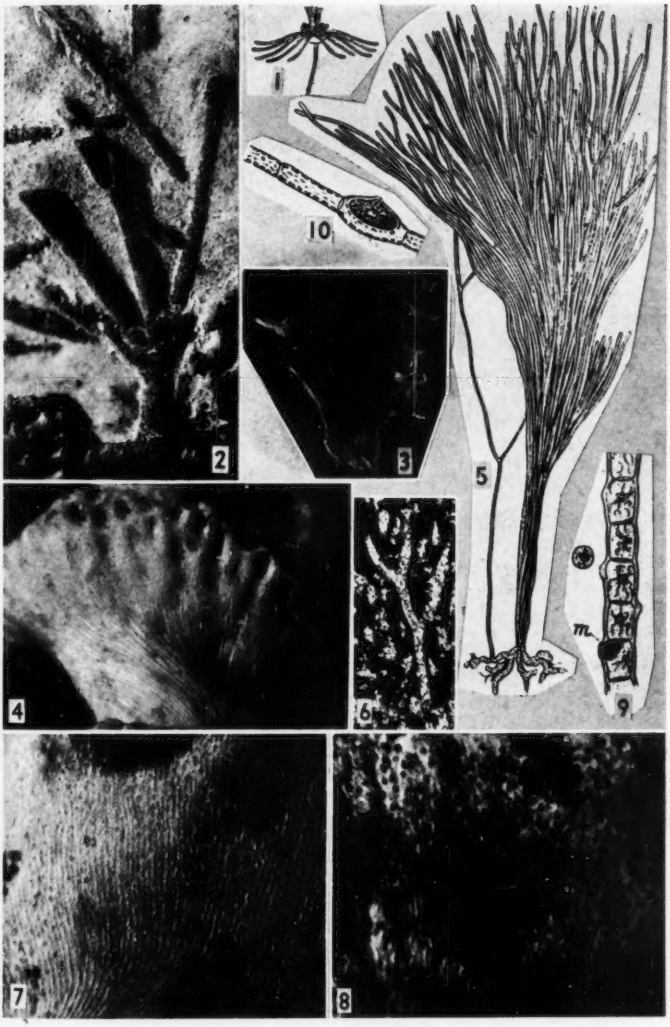
PLATE 1.—1. *Tubularia mesembryanthemum.* Living tubularian hydroid. From Allman, 1872, fig. 84, (part), p. 419; magnification not indicated. 2. *Palaeocoryne,* a symbiotic phytomorph adnate on face of *Fenestella.* One time thought to be a tubularian hydroid, later an appendage to *Fenestella.* Brazer limestone (Upper Mississippian), Flux, Utah. Nebraska Geological Survey collection, ×10. 3. *Archimedes distans* Ulrich. Paired screws twisted in opposite direction, and arising from nearly flat zoarium of *Fenestella serratula* Ulrich. Paint Creek formation, Chester series, west of Chester, Illinois. Modified from Condra and Elias, 1942, Pl. 8, fig. 5, ×1. 4. *Archimedes terebriformis* Ulrich. Part of shaft and lower side of flange of screw. From Condra and Elias, 1942, Pl. 4, fig. 7 × 10. Note fibrous structure of symbiotic phytomorph, which incrusts the fenestrate bryozoan; the fibers of the phytomorph bifurcate at about the same level, thus producing an expanded volume of fibrous tissue in the flange. 5. *Udotea minima,* a living green alga. From Oltmanns, 1922, vol. 1, fig. 252-1, p. 390 (which in turn is modified from A. Ernst, 1904, pl. 7, figs. 6, 7), ×9. Note fasciculation of numerous filamentous thalli, which bifurcate at about the same level, to produce a distally expanded, loosely bundled aggregate; compare with fig. 4. 6. *Ortonella furcata* Garwood. Lower Carboniferous (Mississippian) of England. From Garwood, 1914, Pl. XX, fig. 3 (part), ×55. Note typical bifurcation of filaments in this well established fossil alga; compare with figure 4. 7 and 8. *Archimedes swallovanus* Hall. Detail of flange. Pitkin limestone (Chester) of Oklahoma. Nebraska Geological Survey collection, ×20. Note filaments of symbiotic phytomorph, bifurcating at the expansion from shaft to flange, and developing globuloids (dark spheres), which resemble unilocular sporangia containing monospores of some living algae. Fig. 7 with few, and fig. 8 with many globuloids, and showing faint transverse differentiation of the filaments. 9. *Erythrotrichia ceramicola,* living alga of order Bangiales (now classified with red algae). From Oltmanns, 1922, vol. 2, p. 234, fig. 462-1 (from original illustration by Thuret, 1876).



10. *Rhodochaete parvula*, living alga of same family as fig. 9. From Oltmanns, 1922, vol. 2, p. 234, fig. 462-3 (from original illustration by Bornet, 1892).

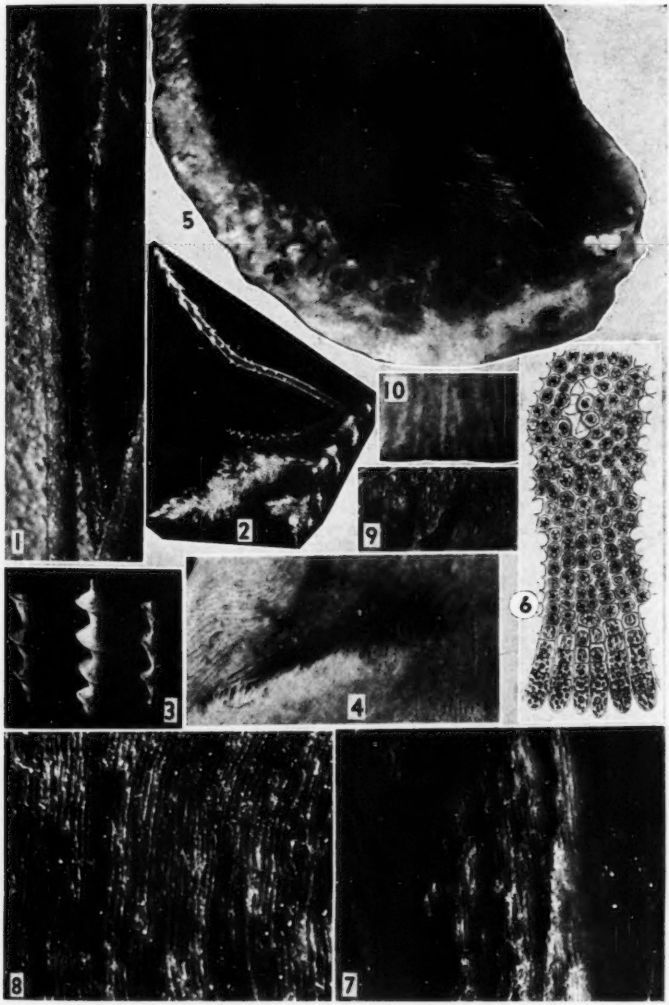
Figures 9 and 10 show development and liberation of monospores from ordinary cells of a simple filament. Compare with figs. 7 and 8. (Scale slightly smaller than indicated.)

the western coast of Europe, after having been introduced while attached to the submerged hulls of ships.

A peculiar double-basket growth-form from the Permian Kaibab limestone of Grand Canyon, which was recently described by Condra and Elias (1945), is another example of phytomorph in intimate symbiosis with a bryozoan. A basket-like bryozoan is encrusted on the inside by a phytomorph. The latter too builds a parallel basket behind the bryozoan basket, the two baskets being interconnected by numerous short uprights. The phytomorph in this consortium resembles morphologically and anatomically the living oriental red alga *Marchesettia spongiodes*. This plant, as yet imperfectly studied, is the only living alga known to form a consortium with a sponge, the plant and animal being intricately interwoven with one another. It was originally described solely as a sponge, but the red alga in it was subsequently discovered, since it constitutes the bulk of the combination.

The well preserved morphology and anatomy of phytomorphic structures are essentially the same in all fossil forms discussed above, and their reference to algae probably would not have been questioned, had it not been for their habitual association with bryozoa. Hence they escaped the attention of paleobotanists. However, in the light of our new knowledge, this association seems biologically understandable, representing a case of symbiosis beneficial to both plant and animal. The results of additional investigations on many other cases of fossil phytomorphs living in symbiosis with bryozoans are being recorded in a series of forthcoming papers.

PLATE 2.—1. *Palaeocoryne*, radiating arms of undescribed American species of this symbiotic phytomorph, adnate on face of *Fenestella nodulosa*. Brazer limestone (upper Mississippian), Flux, Utah. Nebraska Geological Survey collection. ×20. Note fibrous structure and two kinds of ornamentation: larger inverted barbs in upper part of arms, and much smaller, upwardly inclined spines in lower part of arms. 2. *Asparagopsis armata*, a living red alga. From Svedelius, 1933, fig. 7, ×70. Note development of strong, ornamented branches, with inverted barbs in upper part, and much smaller upwardly inclined spines in lower part. Compare with fig. 1. 3. *Archimedes terebriformis* Ulrich. Chester series, near Chester, Illinois. From Condra and Elias, 1942, figs. 21-23. Note excessive twisting in three screws, which results in off-set cork-screw structure and localized bulging, evidence of overtwisting prior to calcification. 4. *Archimedes invaginatus* Ulrich. Pitkin limestone (Chester) of Oklahoma. From Condra and Elias, 1942, Pl. 3, fig. 7 (part), ×20. Detail of overtwisted part of screw to show localized separation of fibers along a groove of constriction, which is next to a bulge. 5. *Archimedes* sp. Pitkin Limestone (Chester), Oklahoma. View of a break across screw. Nebraska Geological Survey collection, ×20. Note radiating and twisted rows of cells in the phytomorph, which is symbiotic with bryozoan, that is seen in cross-section along periphery. 6. *Chorda filum*, one of the most primitive of the living brown algae. Cross-section of a young sporophyte. From Kylin, 1918, fig. 19, about ×200. Compare with fig. 5. 7. *Archimedes wortheni* Hall. Detail of surface of flange. Warsaw formation, at Warsaw, Illinois. After Condra and Elias, 1942, Pl. 2, fig. 2 (part), ×20. Note fibrous symbiotic phytomorph with faint transverse differentiation of the fibers. 8. *Laminaria* sp., living brown alga. From Condra and Elias, 1942, Pl. 2, fig. 1, ×20. Part of blade photographed in translucent light to show filament-like longitudinal rows of cells. Compare with fig. 7 which is of the same magnification. 9. *Archimedes lunatus* Condra and Elias, Pitkin limestone (Chester), Leslie, Arkansas. F. B. Plummer collection No. P-9295,



Bureau of Economic Geology, University of Texas. ×20. Weathered portion of a flange, to show concentric banding of radiating cells, resembling concentric "seasonal" rings of old stipes of living *Laminaria*. 10. *Paleocoryne* sp. from Brazer limestone (upper Mississippian), Flux, Utah. Nebraska Geological Survey collection. ×80. Thin section from near edge of cone-shaped capitulum to show radiating rows of cells with faint transverse and strong longitudinal differentiation. (Scale slightly smaller than indicated.)

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NEBRASKA GEOLOGICAL SURVEY,
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The Relative Value of Taxonomic Characters

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Although taxonomists may disagree on many questions, they are all likely to endorse Crow's (1926) simple statement "that in taxonomy some characters are of greater importance than others." One obvious reason is the fact that experience in identifying plants or dissociated plant parts has taught us to rely on "good" or *diagnostic* characters and to disregard others for this purpose. However, diagnostic characters, though indispensable in identification because of limited occurrence, often prove valueless if applied in the opposite direction toward the construction of classifications. To this end characters of wide occurrence are needed, since their value increases with their constancy in increasingly higher taxonomic categories. Thus our modern systems of classification readily reflect the results of continued observation and study on part of taxonomists, of the kinds of characters, their numbers and distribution in the different groups of the plant kingdom.

At least two sets of characters are, then, constantly used according to the two basic taxonomic procedures: 1) an analytical set for the immediate purpose of identification, composed essentially of diagnostic characters of limited occurrence, and 2) a synthetic set for purposes of classification, represented by fundamental or constant characters of wide occurrence (Diels 1921, Plate 1914).

Another, no less important consideration involves the nature and sources of taxonomic characters. It is safe to say that the majority of taxonomic characters is based on external morphological characters, since they still are the most easily accessible and widely used. Yet they are being supplemented more and more from other sources, i.e., the data of paleobotany, anatomy, cytology, genetics, physiology, chemistry, etc. In short, the aim and scope of phytography have been greatly expanded in keeping with the advances made by other branches of botanical science (Diels 1921, Moll 1934).

Despite the fact that all characters are theoretically of equal value, practicing taxonomists have long recognized differences which result either from the nature of the characters themselves, the organic diversity of the groups of organisms to be classified, or the nature and purpose of the particular taxonomic procedures based on them. It seems, then, that the status and value of any character or group of characters are likely to vary along these lines, as will be shown below.

Significance of Taxonomic Characters in Different Groups

Proper taxonomic treatment of lower plants must of necessity rest on fewer characters than in higher plants. Yet certain characters or character complexes can readily be compared in various groups. It will be clear that a character may be very valuable in the taxonomic treatment of a certain group but does

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not retain this status in other groups (Rensch 1934). For instance, motility by flagella of individual vegetative and reproductive cells provides an excellent character in many algal groups but fails as a criterion in defining the subdivisions of Gymnosperms. The number, type and insertion of flagella found in various algal groups also afford valuable characters, even if they have been appraised differently at different times.

Reproductive organs furnish some of the most widely used and reliable taxonomic characters. Yet the range of variation embraces in this case almost the entire plant kingdom, beginning with the relatively undifferentiated cells of Chlamydomonas and extending to the multitude of distinguishable apomicts in various genera of the Compositae.

Vegetative and ecological characters also deserve mention here. In the delimitation of the well known pteridophyte complex Hydropterideae, the aquatic habit was long accorded greater significance than other characters but the complex has now been divided on the basis of the real relationships of its constituent members with other groups. Similarly, many aquatic members of otherwise terrestrial families of flowering plants have always been classified with their relatives, rather than with other aquatic forms.

Verticillate phyllotaxy and the attendant segmentation of shoots etc. are often useful characters but nowhere are they as well developed as in the Articulatae, a fact recognized in the class name.

Among flowering plants many examples of relative value of characters can be found. For instance, choripetalous forms occur probably more often among members of the Sympetalae than do sympetalous forms among the Choripetalae (Süssenguth 1938). Good examples of critical summaries of the characters used in families and genera are found in Sprague (1939), Rassner (1932), Schwarz (1938), Dormer (1945) and Sun (1946), while every taxonomist can easily add others.

Nature and Significance of Taxonomic Characters

Much has been written about the nature of characters, particularly with reference to lower systematic categories. This controversy was focused mainly on A. De Candolle's classic distinction between *constitutive* vs. *non-constitutive* characters or in modern terminology between *indifferent, fortuitous* or *karyogenetic* vs. *biological, epharmonic, adaptive* or *organismal* characters (Diels 1921, Gates 1921, Sprague 1939). In the opinion of Sprague (1939) this distinction can be made readily in most cases though others are debatable. At any rate, the assumption is that the first group is composed of heritable characters not directly affected by environmental factors, whereas the second group is made up of characters resulting from "adaptations" to the environment. Du Rietz (1930) maintains the interesting and apparently well founded view that many so-called "adaptive" characters are much less influenced by environment than is "generally believed." Fortunately, careful genetical and cytological analyses of transplants grown under varying ecological conditions carried out by experimental taxonomists provide the factual information needed for the final solution of such questions (Diels 1921, Camp and Gilly 1943, Clausen, Keck and Hiesey 1940, Turrill 1940).

Intimately connected with these discussions are others relating to the systematic value of taxonomic characters, i.e., possible differences between infra-specific and specific (quantitative) characters and supra-specific (qualitative) characters. Thus Anderson (1937) concluded "that changes in emphasis are of specific rank, while differentiation separates categories higher than the species." Actually, genetical studies such as those by Goodwin (1945) with two species complexes in Solidago have disclosed no essential difference in the nature of taxonomic characters associated with different taxonomic (infra-specific and specific) levels (see also Mayr 1940). Similarly Haldane (1938) states "Our general conclusion is that there is no evidence that at any rate closely related species differ in a manner qualitatively diverse from varieties. In fact Darwin was correct in regarding varieties as incipient species." Epling (1938) on the other hand was unable to find essential differences between specific and generic characters and character-complexes in the Labiatae.

Closely related species often defy simple distinction by one or a few characters. Anderson and Ownbey (1939) analyzed such a case, *Nicotiana alata* and *N. Langsdorffii*, and determined the presence of eleven genetic coefficients. The latter represent "harmoniously integrated tendencies expressed more or less throughout the entire organism."

So far apparently no complete estimate of the number of characters and genes involved has ever been attempted for any organism. But it seems likely that a large number of almost completely stable genes would have to be included, even though they may tend to escape analysis because of their stability. On the assumption that "these genes, then, most probably would be of the greatest taxonomic importance," Winge (1938) formulated his "hypothesis of stability of genes of taxonomic importance." Another group of genes, the "vital genes" = normal alleles of lethal genes, is considered essential by Winge for the existence of any individual and constitutes an important part of the nature of species. This group of genes is regarded as characteristic of species, genera, and families, and provides the basis for Winge's second hypothesis, i.e., "hypothesis of the taxonomic importance of the alleles to lethal genes." Finally, Winge assumed "that, in substance, those factors which are widely represented in all the chromosomes afford a basis for classification into large taxonomic units; their frequent presence in the chromosomes will entirely prevent a segregation into types in which these factors are lacking . . . ", for which he had formulated his "hypothesis of the taxonomic importance of polymery" (Winge 1923). Thus taxonomists may expect to "find a rough, but only a rough, correspondence between the magnitude of the genetical differences and the taxonomic interval between different groups" (Waddington 1939).

Although "the genetic analysis of taxonomic differences is still in its infancy" (Waddington loc. cit.), taxonomists are not always able to enlist the cooperation of geneticists and therefore have recourse to other methods. These methods can, of course, never take the place of genetical analysis but they can provide much needed information to supplement ordinary taxonomic data. One of these methods is the technique of mass collections which is now widely used (Anderson 1941). (For examples of other statistical methods and their

applicability to taxonomic problems see Anderson and Abbe, 1934 and Boeke, 1942).

Paleobotanists, however, are not always in the position to analyze samples comparable to those commonly available to their botanical colleagues. This is, unquestionably, the reason why the statistical approach has not been more widely used in paleobotany despite its general application in other fields of botanical science. A notable attempt was made by H. Czeczottowa (1933, 1936) in her detailed biometrical analyses of leaves and leaf characters of living and fossil beeches.[1] How successfully statistical methods can generally be applied in the study of the specialized conditions provided by paleontological material has been demonstrated by Simpson and Roe (1939). Finally, the introduction and use of concepts developed in the study of growth in animals, i.e., allometry, etc., are bound to yield unexpected results in the solution of paleobotanical problems (Lumer 1940, Schüepp 1945).

Thus botanists have in some cases attempted to provide new data for special studies, particularly those pertaining to speciation phenomena, or what Richards (1938) has called *taxonomic analysis*. The methods of taxonomic analysis would be in the main tests for homogeneity and would involve series of measurements, linear or otherwise.

Nature and Purpose of Classifications

In his review "On the taxonomic value of the anatomical structure of the vegetative organs of the Dicotyledons" Sprague (1944) proposed the adoption of two separate systems of classification: 1) a practical system useful for catalogues, enumerations, etc., and 2) a system made up of natural groups classed here only after careful scrutiny of all available characters. Whether feasible or not, the main conclusion to be drawn from this is that a completely phylogenetic system can not yet be worked out in view of the inadequacy of available data (mainly external characters) and the need for supplementing these from other sources, provided the added characters are likely to be of permanent value in plant classification. Many taxonomists and paleobotanists would agree "that a phylogenetic and a practical classification are frequently incompatible" (Arkell and Moy-Thomas 1941), a conclusion essentially identical with Sprague's proposal (see also the controversy of Bremekamp 1939, Gilmour and Turrill 1941, and Fosberg 1941). Simpson (1946) claims that in each case phylogeny must first be worked out before classification can be based on it.

A peculiar problem of paleobotanical taxonomy, which it has in common with paleozoology, is "the definition and subdivision of units that have an extension in time as well as in space" (Simpson 1943). Thus vertical units must be recognized in addition to horizontal ones which in turn are based on contemporaneous groups. The taxonomic treatment of vertical units is fully discussed by Simpson (1946), whereas Turrill (1939) suggests the pending difficulties by citing some examples. For instance, the genus Ginkgo and its only living species *G. biloba* lose their clearcut identity, as soon as "the sum-

[1] I am greatly indebted to Dr. M. K. Elias for bringing these references to my attention and for loaning me his copies.

total of known specimens including the known fossils" are taken into consideration. The same problem exists in regard to other isolated genera, species, and intra-specific units that appear distinct in the present flora, since each group is "isolated on the time-scale only by our ignorance of its phylogeny."

As far as the treatment of characters is concerned, Huxley's clines or character gradients must now "be distinguished according to the variate that is used to define the array." "As originally proposed, the idea of a continuous cline is that of a sequence of contemporaneous populations arrayed geographically and intergrading in progressively changing morphological characters" (Simpson 1943). That such clines occur in plants is well known and suitable examples are reviewed by Huxley (1942) (see also Böcher 1944 and Camp 1946). On the basis of the two types of systematic categories, vertical and horizontal, corresponding types of clines are now recognized by Simpson, namely choroclines or "space clines" following geographical arrangement, and chronoclines or "time clines" resulting from temporary arrangement.

Assuming that suitable material can be found, the determination of chronoclines should prove of more immediate value in constructing the phylogeny of minor systematic categories than could be expected by following Zimmermann's procedure of tracing the *phylogeny of single characters* (= Merkmalsphylogenie), so familiar to paleobotanists (Arber 1937). For in Turrill's (1942) opinion "taxonomy is based on characters, phylogeny on changes of characters."

Crow (1926) has shown that all classifications are artificial though in a varying extent. Thus the difference between a truly artificial system and a natural one lies in the number and kind of characters selected, i.e., one or a few characters suffice for artificial systems, whereas many characters of different value are needed for natural classifications. Actually, reasons of expediency may often dictate the selection of characters and the use of subsidiary classifications and nomenclatures, as has been suggested for the treatment of intraspecific entities, etc. (Gilmour and Turrill 1941).

The widely held view that only one natural classification was possible has been challenged by Hayata (fide Du Rietz 1931) who proposed a so-called "dynamic" system, a flexible affair depending on the viewpoint adopted and the reticulate relationships of the characters studied and selected (Du Rietz 1931, Turrill 1936).

The recognition of numerous parallel mutations either "as single characters" or "as shorter or longer parallel series" is certainly most important in the understanding and development of systems of classification (Gates 1936). What can be done in this as well as in other respects through the analysis of characters has been demonstrated by Dickason (1946).

Disregarding for the moment any phylogenetic implications, characters may either be homologous or analogous, a fundamental distinction borrowed from comparative morphology. On morphological grounds characters can and often have been placed in progressive series leading from simple to higher morphological levels. If these series are to be interpreted phylogenetically, it must be remembered, that their arrangement is not uni-directional but actually multi-directional, with the individual series intersecting each other repeatedly and in various directions (Engler 1926). In addition, the personal factor involved in

such appraisals must be constantly checked by recourse to all possible objective criteria. Because the more characters or attributes are assessed in this respect, the closer will be the approximation between the two postulated ideal forms of classification, the purely logical classification based on a maximum number of characters and the truly natural or phylogenetic classification (Diels 1921, Gilmour 1939, Plate 1914).

In conclusion, two general statements can safely be made: 1) every character has potential value, but 2) its real value is always relative, since all taxonomic characters lack absolute value. Rensch (1934) formulated among others the following rule: "Even if the taxonomic value of a character has been 'proved' in a hundred cases, it still may fail in the hundred and first. The golden rule therefore is: there is no golden rule."

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Cenozoic and Mesozoic Bryophytes of North America[1]

William Campbell Steere

The greatest taxonomic problem confronting those who study fossil mosses and hepatics is a paradoxical one—instead of being lumped into form-genera, they have been "identified" with a misleading precision and exactitude. The reasons for this anomalous situation are not hard to find. In the first place, fossil bryophytes are so very rare that they have been described one by one, usually in comparison with living genera, without much reference to earlier descriptions. In the second place, many specimens have been described by non-bryologists who are naturally unaware of modern systematic trends in bryophytes. Furthermore, most of the bryophyte fossils have been named on a local flora basis—the person identifying them has been influenced consciously or unconsciously by the species now inhabiting the region from which the fossil came, in choosing a name. However, as Chaney and many others have shown, there has been a great change in the distribution of floras during Cenozoic times, and one must be familiar with tropical genera as well as temperate ones in order to identify correctly many fossils of Tertiary age.

As a consequence of the casual treatment of bryophytes just outlined, a very heterogeneous assemblage of names has accumulated during the last century. It is time for these fossil species and "fossil" names to be scrutinized and revised by a professional bryologist. I therefore propose to evaluate the species of fossil bryophytes previously described from North America, to arrange them in a systematic order which conforms to present-day ideas on the classification and interrelationships of the Bryophyta, and to revise their nomenclature in accordance with current practice.

Bryophytes are small, relatively simple plants consisting of either a dichotomously branched thallus or a leafy stem. The stems and thalli possess neither lignified wood nor cutinized epidermis, in the sense of vascular plants, and the leaves are very rarely more than one layer of cells thick. The spore-bearing structures are equally uncomplicated, consisting only of a sessile or stalked spore-case. At least, fossil bryophytes do not present the paleobotanist with the difficult morphological and taxonomic problem of correlating a complex series of roots, stems, leaves, cones, fruits, seeds, etc., or still worse, the multitudinous names which have been applied to them in higher plants. The concomitant disadvantage, however, is that the delicate tissues and simple structures of bryophytes leave a poor fossil record. Furthermore, the small size of the plants undoubtedly causes them to be overlooked much more often than they are found.

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1 Paper from the Department of Botany of the University of Michigan.

The correct identification of living bryophytes requires critical microscopic study. Even the distinctions between genera may be based on minute but constant structural features such as the shape and size of cells in different parts of the leaf, stem, or thallus; the presence or absence of papillae on the cells; the structure of cells in the capsule walls; the sculpturing of peristome teeth, and the ornamentation of spore walls. Since these features are ordinarily impossible to distinguish in truly fossilized specimens without the special techniques developed by Walton (1923) and Harris (1931), the confidence of paleobotanists who have assigned different fossil bryophytes to living genera cannot be justified. Furthermore, the appearance of fossilized specimens is certainly highly distorted by the various vicissitudes which they have undergone. For example, the flattened leaf arrangement in most fossil mosses is obviously a result of crushing. The capsules, likewise, of the extremely few fossil mosses whose sporophyte is known, give a fallacious appearance of being extremely wide in proportion to their length. Although these remarks will seem elementary, if not painfully obvious, they seem to be appropriate because of the frequency with which artificial conditions are misinterpreted as representing fundamental generic characters.

In general, Cenozoic bryophytes fall into fairly natural groups, whose difference in preservation parallels their difference in age reasonably closely. For example, the specimens of Tertiary age form one group, since they are almost without exception preserved in a truly fossilized condition, either as impressions or as greatly compressed specimens in which some cellular detail may still be found. Fossil specimens of Pleistocene and post-Pleistocene age which have been preserved in peats, forest beds, interglacial deposits, tufa, loess, clays, etc., form the second category. Since the specimens are "humified" rather than truly fossilized, they lend themselves very easily to microscopic study and identification in the same way that living species do. I have rather recently covered elsewhere (Steere, 1938, 1942) the subject of Quaternary bryophytes of North America, so that they need little discussion here, except to emphasize the importance of mosses in the formation of calcareous tufas, sometimes found as deposits of enormous extent. Furthermore, the usefulness of mosses as indicators of habitat and climate in peat studies has long been overlooked in this country, in spite of the obvious advantage that mosses are deposited *in situ*, whereas the exact source of the pollens so extensively studied must always remain somewhat uncertain.

The time in the geological scale at which bryophytes developed is a real botanical mystery. Many morphologists, starting from the work of Goebel, hold that bryophytes are simplified rather than primitive, and that they may be derived from much more complicated forms. Be that as it may, plant remains from the English Carboniferous deposits are clearly to be referred to the Hepaticae (Walton, 1925). In fact, the specimens are so modern in appearance that Walton was not at first satisfied that they had come from the Palaeozoic shales he was studying and made further preparations until he could be certain. Through later work, Walton (1928) has established the existence of Palaeozoic mosses, although not as conclusively as for the Hepaticae. He says: "Taking the evidence afforded by *M*[*uscites*]. *polytrichaceus*

and *M. Bertrandi* together, there seems to be little reason to doubt the presence of mosses at least as far back as the Stephanian [upper Carboniferous], but what their relationships were to the divisions of the living *Musci* cannot yet be decided. Renault and Ziller considered that their plant showed most points of resemblance to the Polytrichaceae."

There may have been other groups of bryophytes which are now extinct, a view supported by the monumental study of *Naiadita* by Harris (1939). Certainly some groups of living bryophytes are extremely ancient, as shown by their distribution and their morphological structure. Nearly everyone who works with mosses and hepatics develops a feeling of the great age of these plants, perhaps because of the distant relationship between so very many groups. For example, Limpricht (1890) expressed this feeling, as follows: "Gewiss werden die Moose auch in den früheren Perioden der Erdbildung eine ausserordentlich wichtige Rolle in der Vegetationsdecke der Erde gespielt haben, allein ihre zarten Leiber waren für die Erhaltung nicht geeignet . . ."

In view of the paleobotanical and other evidence that perhaps the Musci and certainly the Hepaticae existed in more or less their present form during the late Carboniferous, I do not hesitate to propose that we accept the concept of a continuous evolution of these groups through the Mesozoic and Cenozoic. Consequently, the great similarity of specimens from very different geologic ages need not surprise us. The accompanying table will show the representation of fossil bryophytes in deposits of various ages.

Our species concept of fossil bryophytes must still remain a very elementary one, because of the small number of specimens known, and because of our inability to study large series of specimens and species. Although each fossil specimen is of necessity a species and each fossil genus a receptacle for species rather than a truly natural category, the situation is improved enormously by grouping species and genera in accordance with our treatment of living Bryophyta. For the Mesozoic and Tertiary species of North American Bryophyta I have devised a definite and simple arrangement which can be followed without too much difficulty by the non-bryologist. The system progresses from less to greater complexity, and a species which comes to be better known may be advanced to a position which defines it with more precision. Of course, as more fossil bryophytes are discovered (and I hope that this review will lead to a greater interest in them), further form-genera will have to be established, but it seems to me useless—if not illegal—to manufacture now a series of form-names not represented by specimens.

I can only hope that all the known North American species of bryophytes have been considered here. The literature concerning them is unbelievably scattered, and even the splendid compilation made by Dixon (1927) is incomplete. In view of the bibliographical difficulties in store for anyone who attempts to study fossil mosses and hepatics, I have quoted the short descriptions of species and genera offered by the authors, as well as full citations to place of publication. The kindness of my friends and colleagues, Professors H. H. Bartlett and C. A. Arnold, in offering advice and help is gratefully acknowledged.

SUMMARY OF NORTH AMERICAN FOSSIL BRYOPHYTES.

Age	Plant	Formation	Locality
Miocene	*Marchantites coloradensis*	Dawson Arkose	Colorado
	Jungermannites cockerellii	Florissant	Colorado
	Muscites florissanti	Florissant	Colorado
	Polytrichites spokanensis	Latah	Washington
	Plagiopodopsis scudderi	Florissant	Colorado
	Plagiopodopsis cockerelliae	Florissant	Colorado
	Palaeohypnum arnoldianum	Sucker Creek	Oregon
	Palaeohypnum brownii	Florissant	Colorado
	Palaeohypnum brittoniae	Latah	Washington
	Palaeohypnum patens	Latah	Washington
Eocene	*Marchantites stephensoni*	Upper Wilcox; Fayette	Arkansas; Texas
	Marchantites pealei	Fort Union	Montana
	Marchantites wardii	Fort Union	Montana
	Jungermannites eophilus	Green River Shales	Colorado
	Jungermannites bryopteroides	Fayette	Texas
	Palaeohypnum knowltoni	"Roslyn Sandstone"	Washington
Cretaceous: Upper	*Marchantites yukonensis*	Yukon River	Yukon
	Marchantites sp.	Estevan Sandstone	Sask.-Alberta
	Jungermannites cretaceus	Tuscaloosa	Alabama
	Muscites lesquereuxi	Ripley	Tennessee
	Sphagnum sp.	Patoot Series	Greenland
Cretaceous: Lower	*Marchantites blairmorensis*	Lower Blairmore	Alberta
	Marchantites sewardi	Patapsco	Maryland
Jurassic (Lias)	*Hepaticites laevis*	Thaumatopteris Zone	Greenland
	Hepaticites rosenkrantzi	Thaumatopteris Zone	Greenland
	Metzgeriites glebosus	Thaumatopteris Zone	Greenland
Triassic (Rhaetic)	*Hepaticites amauros*	Cape Stewart	Greenland

A Revision and Suggested Arrangement of the Cenozoic and Mesozoic Bryophyta of North America

Division Bryophyta

Plants with a pronounced alternation of generations, the sporophyte very different from and parasitic upon the gametophyte. Gametophyte thallose or more commonly differentiated into stem and leaves, composed of delicate tissues, always without true roots. Sporophyte consisting of a spore-bearing capsule, usually provided with foot and seta; homosporous.

Class Hepaticae

Gametophyte generally dorsiventral, a thallus or leafy stem, provided with rhizoids. Sporophyte nearly always stalked, usually remaining within the swollen archegonium (calyptra) until mature, the seta elongating only after spore formation; capsule consisting of a wall of sterile cells and a spore-sac; spores often interspersed with elaters.

HEPATICITES Walton, Ann. Bot. 39:565. 1925. "Fossil plants bearing evidence of a relationship to the living Hepaticae, and also exhibiting characters by which they may be distinguished from the Algae, Pteridophyta, and other divisions of the Plant Kingdom, are to be assigned to the form-genus *Hepaticites*, if the knowledge of their structure is too incomplete to warrant the use of a distinctive generic term." *Hepaticites* as a form-genus provides a convenient receptacle for a number of species whose generic position cannot be determined more precisely.

1. HEPATICITES AMAUROS Harris, Meddel. om Grønland 112(2):6. Pl. I, Figs. 7, 9. 1937. (*Ibid.* 85(2): Pl. I, Fig. 2. 1931.) "Thallus 1.5-2.5 mm. wide, branching by equal dichotomy every 3 cm. or less; apices rounded, not markedly attenuated, margins entire. Midrib a rather narrow and well-defined dark strip, not projecting on the surface. Ventral scales absent. Substance of thallus thick, apparently formed by a good many layers of cells which, when pressed together, give no indication of cell rows. *H. amauros* is distinguished from the other Greenland species by its frequent dichotomy, narrow midrib and very thick substance."

Occurrence: Cape Stewart, *A. Hartzi* Bed (Lower Lias and Rhaetic), Scoresby Sound, East Greenland, collected by Tom Harris, 1926-27.

Notes: it is difficult to suggest the relationship of this interesting species, although the figures resemble a number of the larger species of *Riccardia* in the manner of branching. The well-defined, narrow midrib would seem, however, to preclude *Riccardia*, *Blasia*, or *Pellia*. As in the other Greenland species of *Hepaticites*, the apparent affinities are with members of the Jungermanniales Anacrogynae.

2. HEPATICITES LAEVIS Harris, Meddel. om Grønland 85(2):5. Pl. VI, Figs. 7-10; Pl. VII, Figs. 1, 2; Textf. 1. 1931. "Thallus 3.5 cm. long, branched dichotomously at intervals of 1 cm. Angle between halves of a dichotomy 45°. Thallus about 3 mm. broad, composed of a midrib 1.5 mm. broad flanked by a flat lamina .75 mm. broad. Margin of lamina straight, or slightly sinuous, never divided into lobes. Lamina probably composed of only one layer of

cells; cells arranged in rows running from the midrib to the margin. Rows curved so as to meet the margin at nearly a right angle and to meet the side of the midrib at an angle of 60°. Cells largest near the midrib (80μ x 35μ), becoming smaller near the margin (20μ x 20μ). Outlines of cells not very clearly shown. Midrib several cells thick; probably composed of a series of cells continuing the curved cell-rows of the lamina so as to make an angle of 20° between the inner end of a row and the mid-line of the thallus, and of other cells running longitudinally. Midrib sometimes composed of two thick strands separated by thinner tissue. Apices of branches badly preserved but probably rounded. Tissue of midrib less opaque near apex of thallus. No ventral scales seen."

"Rhizoids borne on the midrib, more numerous in lower part of plant; about 4 mm. long and 18-30μ wide, nonseptate and unbranched. Walls of rhizoids without pegs or other ornamentation."

Occurrence: Vardekløft, *Hepaticites* Bed, *Thaumatopteris* Zone (Liassic), Scoresby Sound, East Greenland, collected by Tom Harris, 1926-27.

Notes: this species was based on a single imperfect specimen, so that its structure could not be well determined. It is apparently related to the Jungermanniales Anacrogynae, but without more conclusive evidence, is better retained in *Hepaticites*.

3. HEPATICITES ROSENKRANTZI Harris, Meddel. om Grønland 112(2): 5. Pl. I, Figs. 1-6, 8. 1937. (*Thallites* sp. Harris *Ibid.* 85(2): Pl. I, Figs. 1, 5. 1931). "Thallus attaining a length of over 2 cm.; typically 3 mm. wide (5 mm. in widest parts, 1 mm. in narrowest apical branches). Branching dichotomous and nearly equal occurring at irregular and often long intervals; margin entire or only very slightly lobed. Midrib absent but margins of the thallus usually appearing a little thinner than the middle. Ventral scales absent. Thallus showing two layers of rather similar, parenchymatous cells; cells isodiametric to slightly elongated tending to be placed in longitudinal rows along the middle of the thallus but rows arching outward towards the margin. Actual margins in the apical region possibly only one cell thick but whole of the rest of the thallus showing two distinct layers of cells. Occasional cells of lamina somewhat enlarged and with considerably thickened walls; such cells occurring singly or in patches of three or four, and being most numerous towards the middle of the lamina."

"Surface of thallus (?upper) bearing round or oval cups 1.5-3 mm. in diameter; margins of cup formed of a delicate cellular wall 0.3 mm. high, wall directed upwards from the thallus sometimes overhanging the cup, sometimes pointing slightly outwards, margin entire but seldom well preserved. Base of cup formed of at least two layers of cells, one of these layers and also the sides of cup being very largely composed of cells with thickened walls. Nature of cup unknown."

Occurrence: Neill's Cliff, Liverwort Bed, *Thaumatopteris* Zone (Liassic), Scoresby Sound, East Greenland, collected by Tom Harris, 1926-27.

Notes: This is a very odd plant and probably a liverwort, as Harris concluded, since the areolation of the tissues illustrated is typically that of Hepaticae. The nature and function of the "cup" is very puzzling. Harris says "The cups on the surface of the thallus are an interesting feature; they

might be compared to the gemma cups of *Marchantia* or with the round patches of antheridia or archegonia found on the surface of the thallus of various existing liverworts." The absence of spores or reproductive structures associated with the cups leaves the problem of their nature unsolved. Consequently, although the plants show some affinity to the Jungermanniales Anacrogynae, this species is better left in the form-genus *Hepaticites*.

Order Marchantiales

Gametophyte always a flat, dorsiventral ribbon-shaped, sometimes rather thick thallus which branches dichotomously or by means of intercalary ventral outgrowths; usually with a dorsal, porose epidermal layer, a sometimes chambered green layer, and a compact ventral tissue producing rhizoids and usually scales. Sporophyte spherical and undifferentiated or stalked and dehiscent.

MARCHANTITES Brongniart emend. Walton, Ann. Bot. 39:564. 1925. Fossil Hepaticae with the characters of the order Marchantiales are to be assigned to this form-genus.

1. MARCHANTITES BLAIRMORENSIS Berry, Nat. Mus. Canada, Bull. 58: 34. Pl. IV, Figs. 1, 2. 1929. "Vegetative body thalloid, laminar, of relatively large size, prostrate, dichotomously branched, thickened medianly into a semblance of a midrib, of a thin consistency, and showing in places numerous thin oblique rhizoids. The largest fragment recovered shows part of a body 11 cm. in length and with three dichotomies in this distance. The thallus ranges from 6 to 10 mm in width and has irregularly undulate margins. There are no traces of fructifications."

Occurrence: Locality CH7, Lower Cretaceous deposits of Lower Blairmore Formation, Crowsnest Pass region of Alberta, collected by F. H. McLearn.

Notes: the illustration of this species certainly seems to indicate a species of *Marchantites*. The thallus has about the size and manner of branching of our present-day *Conocephalum conicum*.

2. MARCHANTITES SEWARDI Berry, Amer. Journ. Sci. 200:50. Fig. 2. 1920. "Vegetative body or frond laminar in form, thalloid, without traces of fruiting bodies. The linear, slightly undulate-margined segments fork repeatedly in a dichotomous manner and show a thickened midrib-like portion medianly."

Occurrence: Federal Hill, between North West Branch and Middle Branch of Patapsco River, Maryland, collected by E. W. Berry; Late Lower Cretaceous.

Notes: The illustration [Fig. 2] which has apparently been somewhat retouched, represents a linear, dichotomous thallus which may have affinities with either the Ricciaceae or the Marchantiaceae. On the other hand, it is not altogether impossible for it to have a very different relationship, perhaps with *Metzgeria* or *Pallavicinia*. Since Berry has already assigned this specimen to *Marchantites*, it is probably just as well kept there as transferred.

3. **Marchantites yukonensis** (Hollick) n. comb. (*Marchantia yukonensis Hollick*, U.S. Geol. Surv. Prof. Paper 159:37. Pl. I, Fig. 2. 1930). "A branching frond of unknown size; branches about 5 mm. in width, provided

with a midrib, along the sides of which are minute reticulations that apparently represent the marks of scales."

Occurrence: Upper Cretaceous, Yukon River, north bank about 6 miles above Nahochatilton, collected by A. Hollick and S. Paige in 1903.

Notes: the reticulations are undoubtedly the outlines of the air-chambers characteristic of the marchantiaceous thallus rather than "the marks of scales," which would leave not reticulations, but two rows of parallel, oblique lines, one on each side of the central line.

4. **Marchantites pealei** (Knowlton) n. comb. (*Marchantia pealei* Knowlton, U.S. Nat. Mus. Proc. 35:157. Pl. XXV. 1908). "Thallus of large size, at least 8 cm. long and 1.25 cm. wide, distinctly forking and with the margins erose or erose-undulate; "midrib" broad and diffused with the bundles of closely appressed rhizoids radiating obliquely from it in such a manner as to simulate veins; fruit not preserved. One thing which may militate against its reference to *Marchantia* is the absence of the fine areolations which are so conspicuous in the thallus of the living species. Otherwise it is so close to the living *M. polymorpha* as to preclude the propriety of referring it to other than the living genus."

Occurrence: Hedges coal mine, north side of Yellowstone River, opposite Miles City, Custer County, Montana; lower portion of Fort Union (Eocene).

Notes: The positive comparison with *Marchantia polymorpha* is somewhat surprising, in view of the great similarity of the general appearance of so many genera of thallose hepatics in sterile condition. The lack of areolae mentioned in the description might indicate the genus *Dumortiera*, which in gross appearance does resemble *Marchantia*.

5. MARCHANTITES STEPHENSONI Berry, U.S. Geol. Surv. Prof. Paper 131:4. Pl. IV, Fig. 1. 1922. "Plant body thallose, consisting of a linear, repeatedly dichotomously forked thallus, prominently thickened medianly and with very irregularly placed oblique and transverse markings, which I consider represent appressed rhizoids. The lamina is about 6 mm. wide and the margins are very full and waved. The specimen figured [Berry, 1924, Pl. LXIV, Fig. 2] has a total length of 11 cm. and shows three dichotomies, the left branch of the main fork remaining entire for a distance of 5.5 cm. before forking and the right branch forking at 2 cm.and again 3 cm. and 3.5 cm. farther on. The thallus appears to have been of considerable consistency."

Occurrence: In Eocene deposits, Jacksonville, Pulaski County, Arkansas, Upper Wilcox Formation, collected by Stephenson (Berry 1922); Boggy Creek, Brazos County, Texas, Fayette Formation, collected by O. M. Ball (Berry, 1924; Ball, 1931).

Notes: This seems to be one of the most widely distributed fossil hepatics yet known from North America.

6. **Marchantites wardii** (Knowlton) n. comb. (*Preissites Wardii* Knowlton, Bull. Torrey Bot. Club 21:458. Pl. 219, 3 figs. 1894). "Thallus large, from 8-15 mm. long, and about 6 mm. broad, entire, or more commonly once or twice forked, provided with a distinct midrib which forks with the forking of the thallus, and along the sides of which are numerous vein-like lines caused by the overlapping scales of the lower surface; fruit unknown."

Occurrence: Burns' Ranch, on the Lower Yellowstone 30 miles below Glendive, Montana, collected by L. F. Ward; strata usually referred to Fort Union Group (Eocene), but possibly Laramie (Uppermost Cretaceous).

Notes: The figures look more like a terrestrial form of *Ricciocarpus natans* than *Preissia*, and it is certainly puzzling to consider why it was compared to the latter genus.

7. MARCHANTIA COLORADENSIS Knowlton, U.S. Geol. Surv. Prof. Paper 155:16. Pl. I, Fig. 3. 1930. "Plainly dichotomous, consisting of a main proximad portion about 15 mm. broad, which forks into two narrow distad portions that are 9 or 10 mm. broad and at least 3.5 cm. long. The more perfect of the two branches is rounded at the end, as if it were complete at this point. The entire surface is strongly reticulated, the raised portions of the mesh being relatively thick and strong. The areas enclosed by the raised walls are somewhat irregular, though roughly they are quadrangular or oval. Many of them are now filled with coaly carbonaceous matter, thus proving that the frond had a considerable thickness or substance. Scattered at irregular distances over the surface are strong depressions or pits, now filled with coaly substance, which are interpreted as the points whence rhizoids once arose."

Occurrence: Dawson Arkose (Miocene), dump of Mosby coal mine, Mosby, Colorado, collected by F. H. Knowlton and G. B. Richardson, July, 1910.

Notes: Knowlton interpreted this material as representing the under surface of a vegetative thallus, and that the pits are the points of origin of rhizoids. The illustration (Pl. I, Fig. 3) suggests, however, that the reticulations represent the air chambers characteristic of the Marchantiales, as seen from the dorsal surface. The pits are too irregularly arranged to have any connection with rhizoid formation, and may have no morphological significance.

8. MARCHANTITES sp. Berry, Nat. Mus. Canada, Bull. 63:17. 1930. "A small fragment of a narrowly linear, forked, thallose liverwort occurs in the Estevan beds along a road up a hill . . . It is too incomplete for description."

Occurrence: Estevan sandstone of Upper Cretaceous age, collected by M. Y. Williams in the Cypress Hills district of Alberta and Saskatchewan.

Notes: This specimen is neither illustrated nor described, and is mentioned here only for the purpose of demonstrating areal and stratigraphic distribution of the genus *Marchantites*.

Order Jungermanniales Anacrogynae

Gametophyte dorsiventral, generally thallose, or with indefinite leaf-like lobes, or rarely differentiated into stem and leaves; always without ventral scales; involucre around sporophyte not formed from leaves. Sporophyte dorsal; capsule 4-valved, with multistratose walls, on a rather long seta.

Metzgeriites n. gen. Since no form-genus has been established for fossils recognizable as members of the Jungermanniales Anacrogynae, I propose this name, with the characters of the order, based on the family Metzgeriaceae, which at one time was considered by some authors to include all members of the present order.

Metzgeriites glebosus (Harris) n. comb. (*Hepaticites glebosus* Harris,

Meddel. om Grønland 85(2):4. Pl. I, Figs. 3, 4, 6-11. 1931). "Thallus dichotomously branched; composed of midrib and a lamina. Midrib of uneven width, consisting of slender portions uniting oval areas. Surface of oval areas rough. Under surface of midrib with numerous unicellular unbranched rhizoids which arise from dark swollen cells. Wall of rhizoid evenly thickened. Lamina dissected by more or less deep incisions into irregular lobes, composed of a single layer of cells. Cells of lamina uniform, polygonal, 50μ broad. Cells of midrib elongated. Lobes of lamina usually continuous with one another. Ventral scales absent."

"The substance of the thallus is a delicate brown film on the rock, much more delicate than the associated fern remains. The oval rough areas on the midrib might be taken for sporangia (*cf. Riccia*) but they contain no spores. They might be the places where reproductive organs were produced (antheridia or gemmae), but there is no evidence of this. Like the rest of the axis they bear rhizoids. The divisions in the lamina are quite irregular; the lamina may be undivided, but with an undulate surface (Pl. I, Figs. 10, 11), or divided more or less deeply into lobes which may be entire or divided into two or three subsidiary lobes."

Occurrence: Neill's Cliff, Liverwort Bed, *Thaumatopteris* Zone (Liassic), Scoresby Sound, East Greenland, collected by Tom Harris, 1926-27.

Notes: Concerning the relationship of this hepatic, Harris (1931) says: "This liverwort resembles certain living liverworts, e.g., *Moerckia*, *Blasia* and *Blyttia* belonging to the Jungermanniales Anacrogyneae. Among fossil liverworts it most resembles *H. lobatus* Walton; but it is a larger plant with characteristic rough oval areas on the axis and with a less regularly lobed lamina." Harris' Figs. 6 and 9-11 very closely resemble species of the genera which he mentions as well as of *Symphyogyna* and other related genera now found in tropical America. In view of its undoubted affinities with the present-day Jungermanniales Anacrogynae, it is better placed in the form-genus *Metzgeriites*.

Order Jungermanniales Acrogynae

Plants bilateral, always consisting of a leafy stem; the dorsal leaves in two rows, underleaves present or absent; involucre around the sporophyte formed by leaves. Sporophyte terminal; capsule 4-valved on a long seta.

JUNGERMANNITES Göppert is emended here to exclude the fossil Jungermanniales Anacrogynae which have just been treated under *Metzgeriites*, and is to be reserved for specimens with obvious affinities with the Jungermanniales Acrogynae.

1. JUNGERMANNITES CRETACEUS Berry, U.S. Geol. Surv. Prof. Paper 112:49. Pl. V, Figs. 2, 3. 1919. "Thallus creeping, foliose, dorso-ventral, with a stout flexous axis that bears on its upper surface crowded overlapping ovate orbicular lobes of considerable consistency and about 2 mm. or slightly less in length."

Occurrence: Tuscaloosa Formation (Upper Cretaceous), Shirley's Mill, Fayette County, Alabama.

Notes: The systematic position of this plant is highly problematic, as

Berry recognized: He says: "This unique form is unfortunately represented by only three specimens, two of which are figured. These have been submitted to Prof. A. W. Evans and Dr. M. A. Howe, authorities on the Hepaticae. Prof. Evans dissents from my opinion that the specimens represent a Cretaceous liverwort. Dr. Howe, not forgetting that the remains are problematic, sees a strong superficial resemblance to certain foliose and subfoliose liverworts, as for example, the genus *Chiloscyphus* of our Southern States or the tropical genus *Noteroclada.*

"It must be admitted that the remains are not conclusive, but I know of no vegetative characters that can be shown by a fossil hepatic that are conclusive. They certainly impress the general student, who is less familiar with the details of the living Hepaticae where complete material is available and who therefore does not expect impossible feats of preservation, as remarkably like existing foliose liverworts."

In spite of the somewhat pious remarks just quoted, I am inclined to agree with Evans' opinion that this is probably not a liverwort. The illustrations are ambiguous, and only a careful study by means of modern methods will settle the question. In the meantime, since it is appropriately named, if a hepatic, I propose to leave it here until it can be placed elsewhere with confidence.

2. **Jungermannites eophilus** (Cockerell) n. comb. (*Lejeunea eophila* Cockerell, Proc. U. S. Nat. Mus. 66(19):2. Pl. I, Fig. 1. 1925). "Stem fairly stout, normal, bearing poorly preserved thin rounded leaves, apparently 3 mm. long or less, and well developed bifid underleaves, the latter about three in 5 mm. of stem; underleaves with very stout bases, the lobes more or less unequal, one thick, the other slender, both pointed, with their outer sides convex and inner concave; length of underleaf about 1.5 mm. The specimen consists of about 16 mm. of stem, with leaves."

Occurrence: Green River shales (Eocene), head of East Alkali Gulch, about 8 miles south of DeBeque, Colorado, collected by J. P. Byram, 1922.

Notes: This plant is anomalous in so many ways that it cannot be placed in any genus of living Hepaticae with any degree of certainty or satisfaction. In the first place, no recent hepatic with which I am familiar has unequal or asymmetric underleaves of the type described here. The description indicates that the structure of the fossil may have been misinterpreted, and that the unequally bifid structures are in reality the true leaves or lobes of them, as found in *Cephalozia* or *Lophozia,* that no underleaves are present and that the structures described as "thin rounded leaves" are not part of the specimen at all. Under any circumstances the criteria necessary for the precise identification of the genus *Lejeunea* are not present, since in addition to bifid underleaves, members of this genus must have small folds or lobules on the underside of the dorsal leaves, as well as a certain technical morphology of the perianth. If the specimen is interpreted correctly in the original description, then the "poorly preserved thin rounded leaves" do not show any lobules. In spite of some uncertainty, I believe that this specimen may be placed safely in the Jungermanniales Acrogynae, although no definite generic disposition is yet possible. Cockerell, however, had little doubt concerning the position of his specimen, as his following remarks (1925) will demonstrate: "So far as can be seen, this does not differ from modern *Lejeunea.* Bifid underleaves and

other characters readily distinguish it from *Jungermanniopsis cockerelli* Howe and Hollick of the Florissant Miocene. *Lejeunea eophila* is the oldest known member of the Jungermanniaceae. It might have existed in a tropical or subtropical habitat."

3. JUNGERMANNITES BRYOPTEROIDES Ball, Bull. Agric. & Mech. College Texas, Ser. IV. 2(5):145. Pl. 23, Fig. 2; Pl. 19, Fig. 7. 1931. "Part of the frond of a foliose liverwort, about 4 cm. in length and with a maximum remaining spread of 3 cm. In one specimen the axis bifurcates, certainly twice and apparently three times, at intervals of about one centimeter. The uncertainty in regard to the third dichotomy arises from the fact that a minute fracture in the fossil occurs precisely at the point of forking, hence one branch may or may not belong to the remainder of the thallus."

"The rachis is slender, about .6 mm. wide at lower end of this specimen and 4 cm. higher up is reduced to less than half that width. It was presumably dark brown or black, since much carbonaceous material still remains along its length."

"The leaves are small, crowded, and imbricated; those of the pinnae are irregularly oval in shape and bluntly pointed while those of older parts of the frond are somewhat quadrilateral in outline. In the smaller leaves the margins appear to be smooth but the larger ones have evidently toothed or at least irregular margins. In both cases the inner margins of the leaves overlap and partially cover the rachis or rachilla, as the case may be."

Occurrence: Fayette Formation, Upper Eocene, Boggy Creek, Brazos County, Texas, collected by O. M. Ball.

Notes: The illustrations suggest a leafy hepatic of the order Jungermanniales Acrogynae rather conclusively. Although the leaves are shown to be incubous in the sketch, there is no way of knowing whether the upper surface or the lower surface of the stem is exposed or, furthermore, which is the proximal and which the distal end of the stem. Consequently, until well-oriented specimens are discovered, it will not be known which type of leaf arrangement is shown by this material. In the meantime, the form-genus *Jungermannites* is the most appropriate for the specimens.

4. **Jungermannites cockerellii** (Howe & Hollick) n. comb. (*Jungermanniopsis cockerellii* Howe & Hollick, Bull. Torrey Bot. Club 49:208. Fig. 1. 1922). "Stem ascending at apex; leaves 1-1.5mm. long, 0.4-0.7 mm. in maximum width, contiguous, narrowly spaced, or slightly overlapping at extreme base, the intervals between the leaves commonly resembling the outlines of inverted leaves, the often subfalcate acuminations directed forwards, the acuminations sometimes accentuated by reflexions of the subapical margins, the margins entire or with indistinct indications of small teeth."

Occurrence: Miocene shale, Florissant (Station 14), Colorado, collected by T. D. A. Cockerell.

Notes: The systematic position of this hepatic is quite uncertain, as the specimen is very small and not particularly well preserved. It is somewhat unfortunate that so restricted a generic description was proposed, since if the genus could be retained, it would always have to remain monotypic. In spite of their positive remarks on the relationships of this specimen, the authors apparently still had some reservations as is seen from the following: "Among

the living Hepaticae, the pointed, antically secund leaves of *Jungermanniopsis* suggest the widely distributed *Herberta adunca* (Dicks.) S. F. Gray; but there is no indication that the leaves are bilobed as in the genus *Herberta*. In its antically secund leaves, it resembles also such leafy Hepaticae as *Jamesoniella autumnalis* (DC.) Steph. and certain species of *Nardia;* but in the form and looser disposition of the leaves it is very different from any of these. The possible presence of smaller ligulate or lanceolate lateral leaves might, if fully substantiated, result in placing the plant with the Musci rather than with the Hepaticae. But the small size and general habit of the organism suggest affinities with the Jungermanniaceae rather than with the Musci."

Class Musci

Gametophyte plants always consisting of a leafy stem, the leaves arranged spirally on the stem, rarely in two rows. Sporophyte never imbedded in the tissue of the gametophyte; seta, when present, completing its elongation before maturity of the spores; capsule nearly always with central columella, and dehiscing by means of an operculum; peristome usually present.

MUSCITES Brongniart, Hist. des végétaux foss., p. 93. 1828. This genus was established for those fossils which are clearly mosses but whose systematic position could not be more fully determined.

1. **Muscites florissanti** (Knowlton) n. comb. (*Polytrichum? florissanti* Knowlton, Proc. U.S. Nat. Mus. 51:245. Pl. 12, Fig. 4. 1916). "A single example appears to be a fruiting moss. It has a long, exceedingly slender pedicel fully 2 cm. in length, and a large ovoid capsule that is nearly 3 mm. long and a little over 1.5 mm. in diameter. The capsule appears to be ribbed and somewhat fimbriate at the apex, but this appearance may be due to the state of preservation. The pedicel is practically straight, evidently erect, and the capsule is erect and symmetrical. There is no evidence concerning either calyptra, operculum, or peristome. The ribbed appearance of the capsule suggests a fully mature and more or less shriveled condition after the discharge of the spores. There is no evidence of the presence of leaves. This moss, if it has been correctly interpreted, suggests an old fruiting plant of the genus *Polytrichum*, such for instance as the well-known hair-cap moss, *Polytrichum juniperinum*, but on account of its poor preservation, it is not possible to be certain of its affinity. The generic reference has consequently been questioned."

Occurrence: Florissant lake bed shales, Upper Miocene, collected by Gustavus Hambach.

The excellent photograph of the type specimen, which accompanies the original description of this species does not particularly resemble the sporophyte of a moss, upon cursory examination. In fact, it is far more suggestive of a pedicelled flower, such as that of some maples in the *Acer saccharum* group. This illusion is augmented by the suggestion of branching at the base of the specimen, a condition never found in mosses. An examination of the already enlarged photograph with a good lens demonstrates nevertheless that it almost certainly represents a moss sporophyte. In the original description, Knowlton makes a very cryptic statement that the capsule appears somewhat "fimbriate" at the apex, yet says soon after that "there is no evidence concerning the . . . peristome." The lens, however, reveals a rather well-developed

peristome which, incidentally, is the first discovery of a peristome in North American fossil mosses. The mouth of the capsule shows plainly seven or eight teeth, or exactly the number expected to appear on a flattened capsule bearing a peristome of 16 teeth. Furthermore, there is a suggestion that the teeth are split or bifid for at least part of their length. The number of teeth and their character absolutely preclude any possibility of the genus *Polytrichum,* which has 64 entire, very small teeth. The small stature of this fossil sporophyte is additional evidence against its assignment to the genus *Polytrichum,* whose species are among the largest of our mosses, in both gametophyte and sporophyte. I quite agree with Dixon (1927), who says: "The author compares with *P. juniperinum,* but there can hardly be any reason for selecting this species as the nearest ally." *Muscites florissanti* differs from *Polytrichum* in its small size, and in the lack of an apophysis at the base of the capsule. From an analysis of all available information, I should say that its affinities are with the Dicranaceae, in spite of Dixon's remark that "From the figure it certainly looks like this genus [*Polytrichum*]." However, in view of the ambiguity of the specimen and its lack of gametophyte characters, it is naturally to be considered as a species of *Muscites.*

2. MUSCITES LESQUEREUXI Berry, Bull. Torrey Bot. Club 55:442. Pl. 11, Figs. 1-3. 1928 (*Selaginella laciniata* Berry, U. S. Geol. Surv. Prof. Paper 136:25. 1925 (not Lesquereux, 1875). These small, moss-like fragments were referred to *Selaginella* by Berry (1925) with the remark that "it should be emphasized that the reference of this form to the genus *Selaginella* is entirely problematic and in my judgment entirely without foundation"! Later (Berry, 1928), as the result of studying more material, said: "Study of the new material has shaken my belief that the Ripley form is the same as that from Wyoming. The material is thoroughly carbonized and shows no structural details. I am sure that neither it nor the Wyoming material represents *Selaginella,* and that the former probably represents some moss. In the case of that from the Ripley, of which the accompanying figures give an excellent idea, I have tentatively referred it to the form genus *Muscites* as more likely to represent its botanical affinity."

Occurrence: McNairy sand member of the Ripley formation, Cooper Pit, near Hollow Rock, Carroll County, Tennessee, collected by Bruce Wade (Berry, 1925); R. Lee Collins (Berry, 1928, Pl. 11, Figs. 1-3); Late Cretaceous.

Notes: This is exactly the sort of specimen which should be assigned to the genus *Muscites,* since it cannot be defined precisely, and a more definite name would be as confusing as helpful. The illustration gives an extremely vague impression, but could very well represent a moss.

Order Sphagnales

Protonema thalloid, the gametophyte developing from its edge; branches in fascicles disposed spirally about the stem; leaves composed of a single layer of linear green cells enclosing large rhomboidal hyaline cells. Sporophyte terminal, sessile, globose, with a bulbous base, raised at maturity upon an extension of the gametophyte; operculum present, peristome none, spores tetrahedral.

1. SPHAGNUM sp. Arnold (1932, Pl. IV, Fig. 9) illustrated an unmistakable fragment of the leaf of some species of *Sphagnum* from the upper Cretaceous of Greenland, but makes little mention of this fossil in the accompanying text. The small size of the fragments prevents any attempt to make a definite identification.

Occurrence: In coal, Skansen, east coast of Disko Island, Greenland (Upper Cretaceous), collected by Carl O. Erlanson in 1928.

Notes: This report is of interest since it concerns by far the oldest known specimen of *Sphagnum* from North America. A considerable number of specimens have been recognized and reported from Pleistocene deposits (Steere, 1942), but this is the first to be found in a truly fossilized condition. Dr. Arnold tells me that the *Sphagnum* fragments might possibly have gotten into the coal by accident, because of rough handling in shipment, and mixture with other specimens thereby.

2. SPHAGNUM ANTIQUASPORITES Wilson & Webster, Amer. Journ. Bot. 33: 273. Fig. 2. 1946. "Spores trilete, oblately flattened, circular to slightly triangular in equatorial view. Diameter 23-35 microns; wall 1-1.5 microns thick, smooth, translucent; trilete rays simple, 5-6 microns long."

Occurrence: Kolarich Mine, east of Red Lodge, Montana, Fort Union series of Tertiary age.

Notes: According to the authors these fossil spores are nearly identical to those of modern species and indistinguishable from most fossil forms observed in peat deposits. A careful study of the spores of living mosses, especially of *Sphagnum*, would be very helpful in this connection.

Order Polytrichales

Gametophyte tall, perennial, leaves narrow, with longitudinal lamellae on the ventral surface of the nerve and sometimes also on the back. Capsule sometimes angled; peristome teeth solid, not transversely barred, usually 32-64, derived from several concentric layers of cells.

Polytrichites E. G. Britton apud Knowlton, U.S. Geol. Surv. Prof. Paper 140:24. 1926., emend. I propose that the concept of this genus, which was established for a single specimen, be extended to receive any member of the order Polytrichales which does not represent a now-living genus.

POLYTRICHITES SPOKANENSIS E. G. Britton apud Knowlton, U.S. Geol. Surv. Prof. Paper 140:24. Plate VIII, Figs. 3-4. 1926. "Plants erect or slightly decumbent at base; stems up to 2 cm. high, branching; leaves not crowded except at the summit of the stems, composed of two distinct portions—a paler basal part, which is erect, appressed, and clasping the stem, and an apical part, which is bent outward and spreading, which measures 3 to 4 mm. in length, is evidently strongly veined and keeled, apparently entire and sharply subulate."

"Although much resembling, when magnified, certain living species of *Polytrichum*, the actual size of the plant precludes any definite reference to this genus."

Occurrence: Latah formation, Upper Miocene, Deep Creek, northwest of Spokane, Washington, collected by Henry Fair and C. E. Fernquist, June, 1922 (Knowlton, 1926); "a new locality" (Berry, 1929).

Notes: This plant, which has now been reported from two localities near Spokane, Washington, resembles a *Polytrichum* fairly closely, although the stature of the plant is unusually small for this genus, in which occur many of the largest terrestrial mosses. *Timmia* is another genus with a somewhat similar leaf-structure, composed of sheathing base and spreading lamina. Even though it belongs to a very different family, not at all closely related to the Polytrichaceae, it should not be overlooked.

Order Bryales Acrocarpi

Gametophyte small to very robust; stems usually erect, branching dichotomously or through innovations just below the apex, forming erect tufts or cushions; leaves linear to cordate. Sporophyte terminal at the apex of the stem; capsule usually on a seta; peristome single or double, rarely lacking.

Plagiopodopsis E. G. Britton (1915) emend. Although this genus is not particularly appropriately named, it nevertheless seems to be one of the first generic names established for a clearly acrocarpous fossil moss. Consequently, I propose that our concept of this heretofore monotypic genus be expanded to allow the inclusion of all acrocarpous fossil mosses with the characters of the above order, which cannot be identified more fully.

1. PLAGIOPODOPSIS SCUDDERI E. G. Britton & Hollick, Bull. Torrey Bot. Club 42:10. Figs. 1, 2. 1915. "Plants caespitose, matted together by basal radicles; stem about 1 cm. high, erect, simple or branching; leaves crowded, spreading, about 2 mm. long by 0.5 mm. wide, lanceolate-acuminate, costate to apex; perichaetial leaves longer, extending to or beyond the capsule; seta terminal, 2-3 mm. long, erect and partly exserted; capsule ovoid, 1.5 mm. long by 0.75 mm. broad, erect or inclined, rugose or plicate; mouth 0.5 mm. broad, too indistinct to show any traces of peristome; calyptra and lid unknown.

"It resembles the living species *Plagiopus Oederi* (Gunn.) Limpr. of the Bartramiaceae in size, habit, etc., but is too poorly defined for anything more than identification of its close relationship to the genus *Plagiopus*, as indicated in the generic name adopted for it."

Occurrence: Tertiary (Miocene) shales of Florissant, Colorado, collected about the year 1875 by Samuel H. Scudder (Britton & Hollick, 1917, Figs. 1, 2; Knowlton, 1917, Pl. 12, Fig. 2).

Notes: The original description of this well-preserved fruiting moss was illustrated by a mediocre photograph and some rough sketches. A splendid enlarged photograph was published a few years later by Knowlton (1917), so that there are good illustrations upon which to base some conclusions. Mrs. Britton compared her species with the recent species, *Plagiopus Oederi* and indicated her belief in this relationship by the choice of generic name. It is difficult to agree with her in this interpretation, as *Plagiopus* is a moss with long-exserted, nearly spherical asymmetric capsules, whereas the fossil has an erect, symmetric, ovate capsule, whose seta hardly exceeds the perichaetial leaves in length. This statement may easily be confirmed by comparing the figures just cited with the illustrations of *Plagiopus* (*Bartramia*) *Oederi* in any of the current manuals of American or European mosses.

My conclusion concerning the relationship of this moss is that it is certainly not related to *Plagiopus* and probably not to be placed in the Bartramiaceae at all. It bears a much closer resemblance to certain members of the Orthotrichaceae, which will be seen clearly upon examination of figures of species of *Ulota, Zygodon, Amphidium, Drummondia, Macromitrium* and *Schlotheimia*. In view of the uncertain relationships of this fossil, it is unfortunate that so definite and misleading a name as *Plagiopodopsis* was adopted.

2. **Plagiopodopsis cockerelliae** (E. G. Britton & Hollick) n. comb. (*Glyphomitrium cockerelleae* E. G. Britton & Hollick, Bull. Torrey Bot. Club 34:140. Pl. IX, Figs. 6, 6a. 1907; *Ptychomitrium cockerelliae* Brotherus, in Engler & Prantl, Pflanzenfam. 11:523. 1925). "Plants pulvinate, forming a dark-brown tuft 1 cm. high and 2.5 cm. wide, with lignitic remains appearing like a mass of dark-brown radicles. Stems erect and crowded, evidently branching; leaves 2-3 mm. long, linear-lanceolate, straight or curved, apparently with a thick vein and slender sharp apex; sporophytes terminal, seta erect and straight, 1-1.5 cm. long; calyptra mitrate and plicate, 2-2.5 mm. long, with well-marked ridges forming darker grooves in the light-colored stone."

Occurrence: Miocene shales, Florissant lake deposits, Colorado, collected by Professor and Mrs. T. D. A. Cockerell in 1906.

Notes: This plant, the first fossil moss with fruit recorded from North America, was placed by the authors in a living genus on what seem to me to be insufficient grounds. To quote: "The capsules were not yet developed when this specimen was buried and nothing but the calyptra remains to indicate the nature of the sporophyte, but from general aspect and characters it seems to belong nearest to the Grimmiaceae with a resemblance to the Ptychomitrieae, the calyptra being grooved and long, completely enclosing the sporophyte, as in *Ptychomitrium*, and prolonged into an acute apex as if the lid were rostrate." This is scanty evidence for placing the plant in *Ptychomitrium*, since, in the first place, the calyptra of *Ptychomitrium* is usually deeply lobed or fringed at the base, even when young, and in the second place the leaves are wider, giving the plant a wholly different aspect. This plant, like *Plagiopodopsis scudderi*, reminds me much more of several genera of Orthotrichaceae, which are also characterized by plicate calyptrae. Species of *Ulota, Zygodon, Macromitrium* and *Schlotheimia* grow on rocks as well as on trees. I have seen many specimens of tropical American *Macromitria* which have almost exactly the appearance of Britton and Hollick's Fig. 6a (Pl. IX). As this moss can be placed in the genus *Ptychomitrium* (or *Glyphomitrium*) or any other recent genus only with the greatest doubt and uncertainty, I consider it better placed in a form-genus and so have transferred it to *Plagiopodopsis*.

Order Bryales Pleurocarpi

Gametophyte small to very robust, stems usually creeping, branching irregularly to very regularly pinnate, forming mats; leaves lanceolate to orbicular. Sporophyte lateral on the stems and branches, from very short buds; capsule usually stalked, peristome single or double.

Palaeohypnum n. gen. Since no special name has been applied to fossil pleurocarpous mosses, except the much overworked and most inappropriate

"*Hypnum*," I propose *Palaeohypnum* for members of this order. The modern concept of the now-living genus *Hypnum* is so circumscribed that none of the known fossil mosses approach it.

Palaeohypnum arnoldianum n. sp. (Pls. 1, 2). Stems apparently creeping or floating, much elongated, reaching nearly 10 cm., leafless below, sparsely and irregularly pinnately branched, the branches appearing complanate-foliate, 2-3 mm. wide at the widest part, extending into attenuated, leafless flagellae. Leaves in more than two rows, arranged spirally about the stem, but compressed either naturally or through pressure during fossilization to give a flattened appearance, very regularly erect spreading, 1 mm. long or slightly more, ovate-lanceolate, apparently deeply concave, perhaps keeled, costa not apparent, although its presence is suggested in several leaves. Antheridial and archegonial buds not seen. Sporophyte lacking.

Occurrence: Miocene silts, Carter Creek, near Finley McKenzie ranch house, Malheur County, Oregon; collected by the late Percy Train in 1935. Type specimen: No. 19095, Museum of Paleontology, University of Michigan.

Notes: The abundant and well-preserved specimens are completely sterile and show no traces of reproductive organs, so that no additional light can be thrown on their taxonomic position. The elongated stems and diffuse branching suggest an aquatic moss such as *Fontinalis* or *Leptodictyon*. However, the vascular plants described from the same formation by Arnold (1937) and by Smith (1938) do not indicate much evidence for an aquatic element of the flora, and it may very well be that this was a terrestrial or corticicolous moss which washed into the lake and was preserved. If this interpretation is correct, then there are literally dozens of genera to which this specimen could be assigned on the basis of gross appearance, among which are *Neckera, Plagiothecium, Antitrichia, Pleurozium*, not to mention a number of genera now restricted to the American tropics. In the absence of the microscopic diagnostic features necessary for an exact identification, this moss is placed in *Palaeohypnum* because of its obvious pleurocarpous nature. It is a pleasure to associate the name of my friend, Professor C. A. Arnold of the University of Michigan with this plant, especially since he was instrumental in arranging for the collection of the material.

2. **Palaeohypnum brittoniae** n. sp. ("Moss, genus and species?" Knowlton, U. S. Geol. Surv. Prof. Paper 140:24. Pl. VIII, Figs. 5, 6, 1926). "It consists of several densely leafy stems that it seems to me might be referred to *Polytrichites*, described above, but it has passed under the critical eye of Mrs. Britton, and she considers it too obscurely preserved to permit adequate diagnosis, and it must therefore remain without a name."

Occurrence: Latah Formation, Upper Miocene, Deep Creek, northwest of Spokane, Washington, collected by Henry Fair and C. E. Fernquist, April, 1922.

Notes: This plant is illustrated in Knowlton's paper, but the photograph is so highly retouched that it might perfectly well represent a species of *Juniperus* or some other conifer instead of a moss. The actual specimen, however, which I have seen through the courtesy of Dr. Roland W. Brown, is without question a moss. The specimen is of a pale brown color on a tan, fine-grained

clay, giving altogether too little contrast. Under a good lens, however, with proper lighting, the moss nature of the specimen can easily be seen, although it is too imperfect for a fuller diagnosis.

3. **Palaeohypnum brownii** (Kirchner) n. comb. (*Hypnum Brownii* Kirchner, Trans. Acad. Sci. St. Louis 8:162, 178. Pl. XII, Figs. 4, 4a. 1898). "Stems creeping, forked or divided into nearly opposite branches; leaves ovate lanceolate, acuminate, concave."

"This plant is figured here to show the general habit of the plant. The leaves in most cases are indistinct and only the more solid stems are discernible. The plant seems to be analogous to the recent species *H. populeum*, Sw. The stems are slightly curved and the leaves on some portions are faintly visible. The leaves do not appear to be very closely imbricated."

Occurrence: Florissant Lake beds, Upper Miocene, Colorado, collected by Gustavus Hambach.

Notes: The exact systematic position of this plant has been the subject of a very considerable discussion, although the several botanists who have reëxamined it agree that it probably represents a moss. In the original description, Kirchner compared it to *Hypnum* (now *Brachythecium*) *populeum*, without presenting any convincing reason for so doing. Britton and Hollick (1907) say "It is apparently a moss, but satisfactory evidence of its relationship with the genus Hypnum is not apparent in the figures." Knowlton (1916) reflects this same opinion, saying, "It seems beyond any reasonable question to be a moss, but . . . its reference to *Hypnum* is a matter requiring confirmation. The Scudder collection contains a single fragmentary branch that appears to belong here." Dixon (1927) says "The author compares it with *Brachythecium populeum*, but the figures do not suggest that, the leaves being broader and shorter. "Brachythecioid" seems as near as it seems safe to go."

I cannot see much resemblance to *Brachythecium* in the illustrations (Kirchner, 1898; Britton & Hollick, 1907), but a closer approximation to the branching of *Hylocomium* and other genera. Finally, it is obvious that this plant is not satisfactorily maintained in the genus *Hypnum*, which has been gradually restricted by the removal of different elements until now all members have secund or falcate-secund, ecostate leaves. As a consequence, this fossil must be transferred to the form-genus *Palaeohypnum*.

4. **Palaeohypnum patens** (E. G. Britton) n. comb. (*Archaeomnium patens* E. G. Britton apud Knowlton, U. S. Geol. Surv. Prof. Paper 140: 24. Pl. VIII, Fig. 1, 2. 1926). "Plants up to 2 cm. high by 3 mm. broad; stems simple or branched, erect, apparently tomentose, with one branch bearing a curved, leafless apical prolongation about 1 cm. in length; leaves crowded and spreading, larger and more numerous at the apex of the stems, lanceolate-acuminate, about 1.5 mm. long by 0.5 mm. broad, seemingly entire and costate to apex, with revolute margin."

"Resembles the living species *Aulacomnium palustre* (Linné) Schwaeger. in the leafless prolongation of the stem with a slight induration of a capitate tip, the presence of tomentum, and the larger crowded apical leaves."

Occurrence: Latah Formation, cut No. 1 on Spokane, Portland, & Seattle Railway, Spokane, Washington, collected by Henry Fair and C. E. Fernquist, June, 1922; Miocene deposits.

Notes: In spite of Mrs. Britton's comparison of this moss to *Aulacomnium palustre* (and the indication from the generic name that it is related to the general *Mnium* series), its affinities can hardly be with the latter species or even the genus, as the leaves are too short, too wide, too broadly spreading, and their disposition on the stem is entirely different. In fact, although the leaf shape and nervation suggest a few species of *Bryum* or even *Mnium*, as the generic name indicates, the specimen, from its manner of branching, as well as the arrangement of leaves, is better placed in the pleurocarpous series.

Certain species of *Plagiothecium*, although completely lacking a costa, have much the same appearance, as do many species of *Rhynchostegium*. *Palaeohypnum patens* resembles *P. arnoldianum* described here, but differs in the more widely-spreading leaves and lack of costa. I am convinced that this is not an acrocarpous moss and therefore transfer it to the genus *Paleohypnum*.

5. **Palaeohypnum knowltoni** (E. G. Britton) n. comb. (*Rhynchostegium knowltoni* E. G. Britton, Bull. Torrey Bot. Club 26:79. 1 fig. 1899; Britton & Hollick, *Ibid.*, 1907, Pl 9, Fig. 5).

"Stem 1 cm. or more long, showing as a carbonized line at several points and seemingly continuous with a slender, curved, carbonaceous prolongation from its apex, like a leafless stolon. Leaves about 1 mm. long, one-third as broad, becoming smaller toward the apex of the stem, more or less two-ranked or flattened, spreading at an angle of 45°, not crowded nor overlapping, unequal at base, the upper half of the leaf rounded at base and covering the stem, the lower narrower and tapering to the stem; vein indicated or suggested more or less clearly in the lower leaves by carbonaceous lines continuous beyond the middle of the leaf, disappearing below the apex which is acute but somewhat blunt, in some leaves quite rounded and broad, not tapering."

"Evidently belonging to the Hypnaceae with flattened, apparently two-ranked leaves, suggesting by its tapering, stoloniferous stems a species related to *Rhynchostegium rusciforme* (Neck.) Br. & Sch., but differing from that species in its more flattened less crowded leaves and more slender stems."

Occurrence: Obtained by Prof. I. C. Russell at a coal mine one mile west of Cle Elum, Kittitas County, Washington, July 7, 1897, from "Roslyn Sandstone," probably Lower Miocene or Upper Eocene.

Notes: This moss has been sketchily, though probably accurately figured (Britton, 1899; Britton & Hollick, 1907) and the description is unusually complete. Its position in the Musci is not clear at all, in spite of the apparent confidence with which Mrs. Britton placed it in a living genus, with the remark that "This fossil species has therefore all the essential characters of the genus, though differing somewhat from all living species." I consider these to be very insufficient and only presumptive reasons for a generic identification and so transfer the species to the form-genus *Palaeohypnum*. Most mosses, under unfavorable conditions, will produce flagelliform, attenuated branches, whereas they are normal in other species, especially in members of the Neckeraceae.

Excluded Species, Genera, and References

Many fossil specimens have been referred to the Bryophyta through error and through incomplete knowledge of the specimen. Many of these errors

have gradually been corrected in the literature; others have escaped until now. A list of names which should be excluded from fossil Bryophyta follows:

1. CHRYSOTHECA Miner, Amer. Midl. Nat. 16:590. 1935. "Plant body small, smooth, ovate, oblong-ovate, or lanceolate, with few to several plications, sessile or apparently short stalked; mouth fringed or slightly laciniate." This genus was proposed under the heading "Bryophyta."

C. DISKOENSIS Miner, loc. cit., Pl. 18, Figs. 1-10. "Plant body smooth, ovate, oblong-ovate, or lanceolate, 232-348 x 680-1029μ, generally 280 x 796μ, 3-6 plicate to the base, sessile or apparently short stalked, mouth slightly fringed."

Occurrence: In the Upper Cretaceous coal, Amisut, east coast of Disko Island, Greenland, collected by Carl O. Erlanson, in 1928.

Notes: The interesting structures upon which my friend, Dr. Miner based his genus *Chrysotheca* are interpreted by him as resembling the perianths of many of the Jungermanniales. Since no traces of the vegetative parts of Hepaticae were found among his material, and since perianths have not been found associated with the abundant liverwort fossils discovered in Greenland by Harris (1931, 1937), it is considered advisable to exclude *Chrysotheca* from the Bryophyta. During the course of his studies, Dr. Miner showed me many specimens of *C. diskoensis,* and although at the time I had no idea of their relationship, it seems to me now that they perhaps represent small seeds or fruits. The achenes of many Compositae present a very similar appearance because of their columnar, fluted structure.

2. DISCITES MINUTUS Harris, Meddel. om Grønland 85(2):6. Pl. VII, Figs. 4, 9; Textf. 1. 1931. "Fossil consisting of a flat disc, 4 mm. in diameter, divisible into an inner homogeneous area of 250μ diameter bordered by a cellular zone of about 83μ radius, sharply delimited from the inner area. Outer zone only one cell thick; cells polygonal, 10μ in diameter. Walls of cells straight and rather thick. Marginal row of cells more clearly shown than the others. Substance of disc very thin and fragile, soluble in $HNO_3 + KClO_3$ followed by alkali. Many specimens of this fossil were seen, the best ones were found in the mud obtained from the preparation of the balsam transfer of *Hepaticites laevis;* they were, however, so delicate that most of them were damaged in being mounted. Others were found still adhering to the transfer, and are closely associated with certain branches of *H. laevis.* The association suggests that they may either be organs of this liverwort, or part of an organism biologically associated with it."

Occurrence: Vardekløft, *Hepaticites* Bed. associated with the type specimen of *Hepaticites laevis, Thaumatopteris* Zone (Liassic), Scoresby Sound, East Greenland, collected by Tom Harris, 1926-27.

Notes: In view of the uncertainty concerning the nature of this fossil, in spite of its close association with a hepatic, it can hardly be assigned a position in the Bryophyta at present.

3. FONTINALIS PRISTINA Lesq. in Hayden, Rept. U. S. Geol. Surv. of Territ. 8:135. Pl. XXI, Fig. 9. 1883. In the original description of this species, which came from the Upper Miocene beds of Florissant, Colorado, Lesquereux (1883) does not qualify his assignment of it to *Fontinalis* in any

way. Britton and Hollick (1907) are the first who seem to have questioned the identification, but passed over it with the note that "it may be merely remarked that the correctness of its reference to the genus *Fontinalis* is questionable, so far as may be judged by the figures." The problem of the identification of this fossil was finally solved by Knowlton (1916). His remarks are so enlightening that they are worth quoting here at length (footnote, p. 245): "In the Scudder and Hambach collections there was found several specimens that agree perfectly with the figures given by Lesquereux, and without special study they were referred to *Fontinalis pristina*. Later, however, a specimen was noted that showed conclusively that it is a *feather* . . . It has been submitted to a number of ornithologists . . . who indorse this reference without qualification. . . . If there had been present only the upper half of the above described feather it would have been identified at once as Lesquereux's *Fontinalis pristina*, for it would then be indistinguishable from the original figure as well as from specimens usually so identified, but being preserved entire, as it is, its avian character is at once apparent." Knowlton's positive statement is approved by Dixon (1927) and by Dr. Roland W. Brown (personal communication of Nov. 18, 1937), so that this name needs no further consideration by bryologists.

4. HYPNUM COLUMBIANUM Penhallow apud Dawson, Trans. Roy. Soc. Canada 8(4):77. Fig. 3. 1891. The specimen from the Lower Tertiary of British Columbia, as represented by its illustrations (Dawson, 1891, Fig. 3; Britton & Hollick, 1907, Pl. IX, Fig. 4) is so poorly preserved and in so incomplete a condition that if it were a moss, it could not be placed at all definitely. Britton and Hollick (1907) express the opinion that this "is more likely a conifer, apparently related to *Widdringtonia helvetica* Heer . . . or to *Glyptostrobus Ungeri* Heer," an opinion quoted with apparent agreement by Dixon (1927).

5. HYPNUM HAYDENII Lesq. in Hayden, Ann. Rept. U. S. Geol. Surv. Territ. 1874, p. 309. 1876. Two years after its original publication, Lesquereux (1878), who was a capable bryologist, published illustrations of his species as well as further notes. After comparing *Hypnum haydenii* with *H.* (*Rhytidium*) *rugosum* and *H.* (*Cirriphyllum*) *Boscii*, he says "The mode of division of this plant separates it from the Lycopods, while the apparently thick leaves seem abnormal for a species of moss." In 1902, Knowlton suggested that this species should be referred to *Lycopodium*. The second difference of opinion was voiced by Britton and Hollick (1907), who said (footnote, p. 140): ". . . the type specimen of *Hypnum Haydenii* was transmitted to us for examination, from which our figures were made. We are satisfied that it is not a moss, and . . . it can not be a *Lycopodium*. The closest comparisons which we have been able to make are with certain conifers, especially with forms of *Juniperus communis* L., in which the young growing branchlets often present a striking similarity in general appearance to this specimen." Stimulated by the remarks just quoted, Cockerell (1907, 1908) found that *Hypnum haydenii* agreed exactly with a later-published species of *Sequoia, S. affinis*, and made the new combination, *S. haydenii*. Knowlton (1916, 1919), apparently unaware of Cockerell's disposition of the species, made the combi-

nation *Juniperus? haydenii*. Under any circumstances, it would seem that *Hypnum haydenii* of Lesquereux is a conifer and not a bryophyte.

6. LYCOPODITES MEEKII Lesq. (1879) and
LYCOPODITES UNCINATUS Lesq. (1879). Solms-Laubach (1891) suggested that these two species might be mosses, an opinion which has received little encouragement, and which has been contradicted by Seward and Dixon (1927). An examination of the modern literature shows that in the current usage of paleobotanists, these species are excluded from the Bryophyta.

7. MARCHANTITES ERECTUS (Bean) Seward, of Ward, U. S. Geol. Surv. Mon. 48:53. 1905. Ward himself doubted that this specimen represented the English plant, and it is still more doubtful if this specimen from Douglas County, Oregon, is a hepatic. Ward says: "The mode of branching of it is similar to that of *Brachyphyllum* and the plant may be really a twig of that conifer." In view of the relatively good preservation and easy recognition of the remaining American species of *Marchantites*, it will be much better to ignore this very doubtful one. If it cannot be identified as the twig of some conifer, then it might be transferred to the genus *Thallites*, as Walton (1925) has done with European specimens.

8. THALLITES Kidston ex Walton, Ann. Bot. 39:564. 1925. "Fossils in which the plant body is of a thalloid form, as may be found in the Algae, Bryophyta, or sometimes in higher groups; but possessing no characters by which they may be assigned to any one of these groups to the exclusion of all the others."

THALLITES sp. Harris (1931) = *Hepaticites Rosenkrantzi* Harris (1937).

9. Microfossils of bryophytic affinities are reported by Bradley (1931) from oil shales of the Geen River Formation of Colorado and Utah (Middle Eocene). He records that "Spores, sporangia, annuli, and scattered fragments of tissues of mosses and ferns are also found in the oil shale and in chert concretions." Under the heading "Moss and Fern Spores" he describes and illustrates (Pl. 23) many types, of some of which he says "These spores resemble spores of some of the Marchantiales." Bradley furthermore illustrates (Plate 24, Fig. 1) a puzzling structure with the following remark: "This tapered filament strongly resembles the tip of an outer peristome tooth of one of the Bryales." One of the most neglected fields of bryology has been the study of the comparative morphology of spores, with a view toward their use in the identification of species or larger groups. Consequently, with the exception of *Sphagnum* and certain genera of Hepaticae, whose spores are occasionally recognized, it is impossible to evaluate the identification of the spores illustrated by Bradley. Aside from the problematic identification of the material illustrated, with which few bryologists could agree, the probability of the occurrence of a single peristome tooth in oil shales seems to me very slight.

10. "Structures simulating bryophytic antheridia" were reported from Upper Cretaceous coal from Greenland by Arnold (1932, Pl. IV, Figs. 2, 4, 7). Further studies by Arnold and by Miner (1935) have shown that these structures are derived in all probability from small seeds of higher plants, and they have accordingly been assigned to the form-genus *Spermatites* Miner.

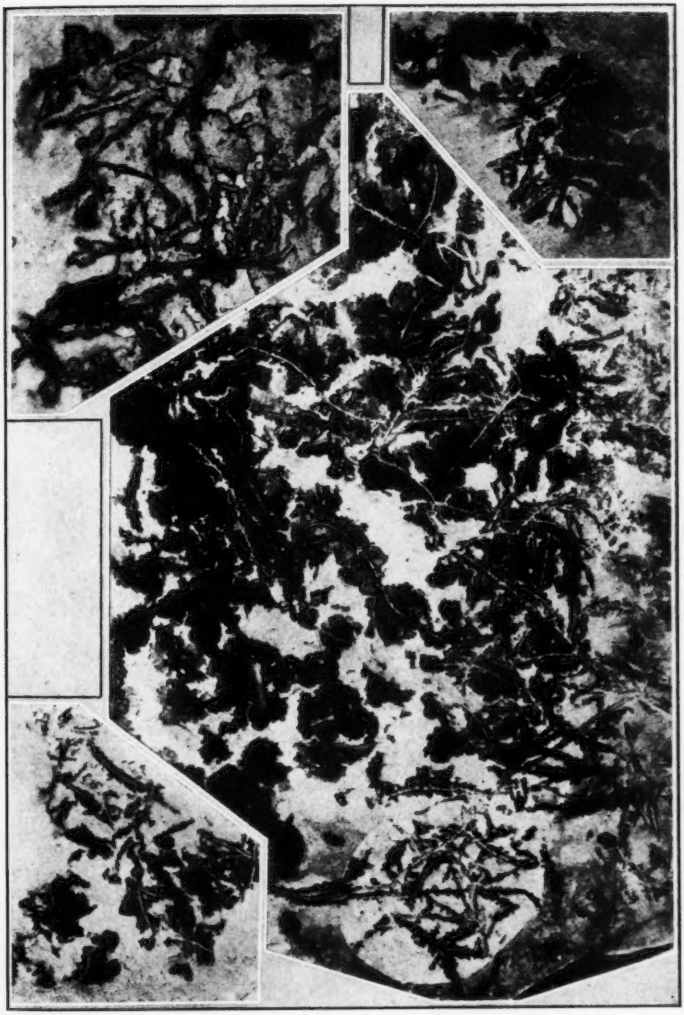

PLATE 1.—*Palaeohypnum Arnoldianum* Steere, ×1. Photograph by C. A. Arnold.

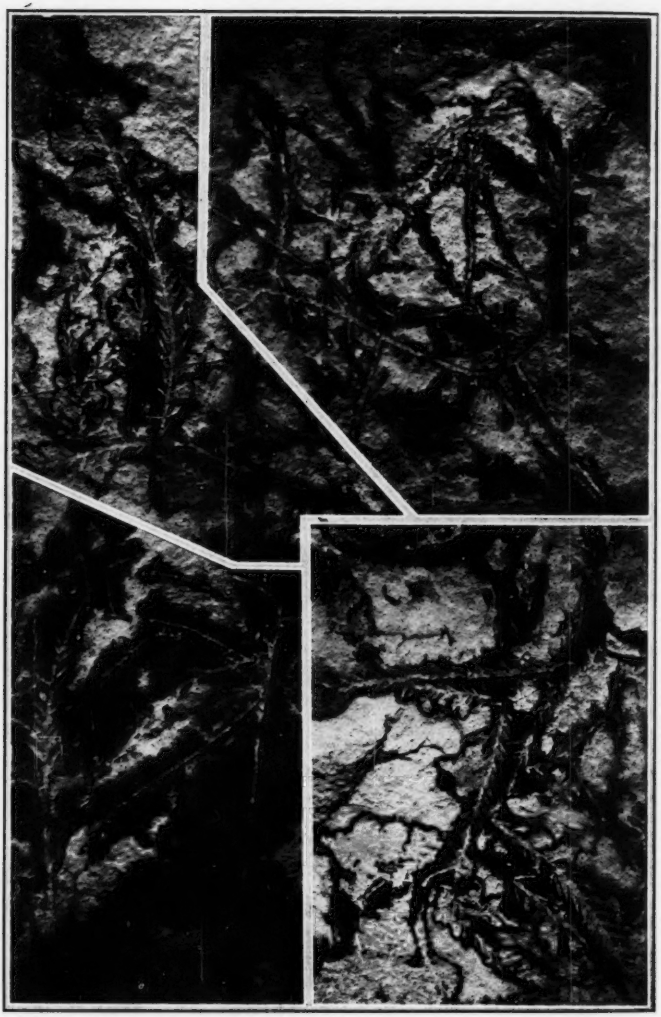

PLATE 2.—*Palaeohypnum Arnoldianum* Steere, ×2. Photograph by C. A. Arnold.

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The Taxonomic Treatment of the Fern-Pteridosperm Complex

Norman W. Radforth

The expression Fern-Pteridosperm Complex has been used to include the fossil ferns and the groups now known as the Lyginopterideae and the Medulloseae. It also embraces those fossil plants known chiefly by their foliage and often referred to as fern-like plants. Its members are distinguished in that many have served as reference entities in phylogenetic, palaeoecological and geological studies—mostly in fundamental science but occasionally in applied. They have contributed with significance in problems concerned with the ancestry of modern plants, the history of form and function, the study of plant migration, the study of climatology, and have served as stratigraphical and time indices.

My present purpose is to discuss modern Taxonomy in relation to this important group of fossils. By referring to it as a group it is not intended that it should be regarded as a taxonomic entity. Long before our knowledge of the group was as complete as it is today its members were marked as designating the carboniferous as the age of the ferns. Discovery later seemed to sanction a new designation for the same period, the age of the Pteridosperms, elevating as it were a vast flora to the Spermatophyta. There have been, however, those who hesitate in accepting the latter, and with good reason. There was justification for a view that some, perhaps a large number of non-seed-bearing fronds discovered in the Carboniferous, though similar to the seed-bearing ones, probably belonged to the true ferns, not to the Pteridosperms, e.g., species of the former genus *Dactylotheca* (Radforth, 1942).

As Turrill states (1936), taxonomy is "the law of order." The basis of the order in the Fern- Pteridosperm complex is not only so elusive as to have been responsible for the above mentioned vacillation of opinion, its very elusiveness is the chief cause of frustration for the taxonomist who would prescribe the law. Yet, by reason of the great usefulness of the group this law must be formulated and administered.

Survey of the Material

Let us examine the material within the complex, and with which the taxonomist and morphologist must deal. It is not constituted of plants, but of parts of plants—organs in the broadest sense of the term, and often ill-preserved.

The true botanical character of these fragments is altered accordingly as they are preserved as impressions, compressions, mummifications or petrifactions, and also accordingly as the matrix in which they are held is constituted.

Finally, should the botanical character of the fragments be successfully interpreted, and an attempt be made at reconstruction of organisms from

apparently related parts it may obtain that the latter occurred in widely separated horizons geographically and geologically.

Thus it is the lot of the taxonomist to deal with plant fragments, at the best modified in preservation and representative of different times. The question arises: Can he legitimately administer to material of this nature as he could with modern plants?

The Modern Taxonomy

Before this question can be dealt with it would be well to enquire whether modern taxonomy is prepared to recognize the problem, and if so, how this problem is to be met.

Verdoorn (1938) wrote: "The old fashioned taxonomists were interested to a limited degree in the morphology, anatomy, distribution and economic uses of their plants. Nowadays, however, it is impossible to carry out successful taxonomic research without a thorough knowledge and a real understanding of the experimental morphology, cytology, ecology and general biology of the group with which one is working."

Huxley (1940) states: "The very success of taxonomists in collecting material from all parts of an organism's range, in separating and naming groups, and of drawing ever finer distinctions has thrown up a number of general questions which must be answered if taxonomy is to find principles which will enable it to cope with the vast burden of its own data, and to advance to the status of a fully-fledged sub-science in which observation and theory, deduction and experiment all contribute to progress."

Both of these statements offer encouragement in that they reflect a broadening of viewpoint among taxonomists suggesting perhaps that consideration of ancestral groups is necessary for a complete taxonomic picture of the plant kingdom.

If adequate taxonomic treatment is to be given to the Complex, and for that matter to other groups of fossils, the point will have to be settled as to whether the system of classification should be phylogenetic, natural or artificial. Bearing on this problem is the conclusion of Bremekamp (1931): "A natural system of classification of organisms is an illusion and the construction of a phylogenetic tree is an impossibility. Palaeontology has contributed little to the development of the present classification. . . . Recognition of affinities between larger groups (e.g., Pteridophytes and Spermatophytes, etc. . . .) has come through comparative morphology not through palaeontology." Arkell and Moy Thomas (1938) present a different view: "The method of classification now used by the maiority of palaeontologists is the phylogenetic one, in which fossils are arranged as nearly as possible in accordance with the supposed course of their evolution. Thus classification has come to aim not only at providing an easy means of recognizing fossils, but also at giving a summary of existing knowledge of phylogeny." ". . . the conclusion is that we can only retain a system of classification and of nomenclature that shall perform its chief function of being useful if we broaden its philosophical basis and recognize that it must assimilate categories of different meaning and different value in different groups." . . . "any System that can be devised is of necessity so

artificial, and so far from coinciding with Nature, that there is no reason for crippling ourselves with rules and restrictions which would rob the existing System of its useful elasticity."

Phylogeny then is not to precede taxonomy though it is not to be divorced from the system. Basically, however, the system could still be a natural one as opposed to the last possibility—an artificial system. A natural system is one which groups together individuals which have a large number of attributes in common, and an artificial one groups together individuals having a small number of attributes in common (Huxley, 1938).

It is clear that the fossils are specimens which lend themselves best to treatment according to a natural system as defined above. Arbitrary selection of attributes is surely the best if not the only method of working out the basis of taxonomic laws. Indeed is this not the usual practice in palaeobotany? If phylogeny is expressed, it is because the natural classification so often reveals it. Certainly so far as the Fern-Pteridosperm Complex is concerned I see no great difficulty here.

The difficulty arises when the International Rules of Botanical Nomenclature, the regulations on which the system is based, are applied. The reasons are chiefly those already expressed in the discussion of the nature of the material to be classified. It might be held, for example, that a fragment of fossil wood can be relegated to a legitimate genus and species on the basis of a consideration of gross anatomy, ray, tracheid and pit characters. One who diagnoses wood of modern plants, however, might indicate that this is inadequate for designation to valid genera and species. M. W. Bannan expresses the view that: "Because of this great variability in wood structure, it is clear that anatomical studies must be based upon wide selections of material if they are to have taxonomic value." Thus it may be interpreted that Lyginopterideae cannot supply the attributes to warrant genus or species designation.

The difficulty of application of the Rules is expressed also in the well known case of *Calymmatotheca Hoeninghausi* Bgt.

Proposed Emendations to the International Rules of Nomenclature

In dealing with certain members of the Fern-Pteridosperm Complex the author experimented with the proposed additions to the International Rules suggested by European palaeobotanists (Jongmans, Halle, Gothan, 1935) (Thomas, 1935). Their proposals for the establishment of organ genera, artificial (form) genera and combination genera contribute towards settling many taxonomic difficulties within the group. It will be recalled, however, as indicated by Florin (1938) that there was disagreement on the point of determination of types at the time when these proposals were being considered as emendations to the Rules. These emendations when put to the test, provide, as Florin again shows (1938), at least a workable basis for a system of classification. The system must be considered as subsidiary to the main one to which the legitimate Rules prescribe. This is in accordance with one of the aims of the Association for the study of Systematics in Relation to general Biology (1937) which is: "To consider how far in the light of cytogenetic,

ecological, physiological, embryological and palaeontological data, existing classification might require to be modified, and new subsidiary terminology to be introduced. Further, to investigate the relation of any such subsidiary terminology to the International Rules of Nomenclature."

It would seem advisable that every case tested by application of the subsidiary rules suggested in Europe should be considered by a responsible committee. The writer would be happy to submit to any such committee established by this Section its first problem, the Taxonomy of the genus *Senftenbergia*. It was of interest to the writer to consider the possible taxonomic status of this genus both before and after its members had been critically examined with modern palaeobotanical techniques. The following conclusions seemed to obtain.

Before Application of Techniques; See Rules: Jongmans etc. (1935); Thomas (1935).

1. *Senftenbergia* cannot be regarded as an artificial (form) genus because its species are related.

2. *Senftenbergia* cannot be regarded as an organ genus because it is stipulated that the organ (singular) must be clearly established.

3. *Senftenbergia* is not a combination genus.

4. *Senftenbergia* cannot be regarded as a natural genus because it is still a fragment.

After Application of Techniques;

1. New methods brought to light numerous attributes hitherto unnoticed with regard to

   a) pinnule morphology (e.g., incurved margin).
   b) anatomy of hairs.
   c) sporangial position, form, size.
   d) morphology of annulus.
   e) spore development, character, size, and number.

2. *Senftenbergia* is still not an artificial genus though diversity of form has been revealed. Species are still related.

3. It is not an organ genus. Examination of the list of attributes makes it more difficult than ever to select *the* organ.

4. It is still a category based on plant fragments. As the matter stands therefore it is still not a natural genus. However, by reason of its increased number of attributes it is a category which is clearly related to a taxonomically valid genus *Anemia* which *is* a natural genus. Indeed, on these ground could it not be made valid that *Senftenbergia* is a natural genus?

5. Which species is the type? If this must be established, the writer is inclined towards the view of the British palaeobotanists (Thomas, 1935). However, does this necessity arise? In designating a new specimen which shows *Senftenbergia* affinities it is hardly desirable that reference should be made only to the first described species as the type when new methods have revealed fundamental attributes in the other species. On the contrary, it is desirable to refer to all species that have been included in the category.

In connection with other members of the Fern-Pteridosperm Complex with which the writer has been concerned the taxonomic value of the name of the category is not so evident. According to the additions to the Rules these

would probably be regarded chiefly as organ genera, e.g., *Asterotheca*. Here the term organ is used in the limited sense. However, it is not at all certain that the species within this category are related to the extent that they should be included under a single taxonomic unit (Andrews, 1943). On these grounds perhaps it would be more useful to regard *Asterotheca* as an artificial genus. The important point is that the investigator makes it clear that the category is not to be regarded as a natural genus. The term artificial is quite suitable so long as the regulation to indicate the type is laid aside. The latter recourse was suggested by Florin (1938) in his work on the so-called organ genera associated with *Walchia*. On the basis of the justification for subsidiary classifications (Huxley, 1938) this suggestion would stand.

It is safe to predict that the application of modern technique to other members of the Complex will reveal greater numbers of attributes. If these numbers are large enough on the strength of the taxonomists' definition of "natural" and the appeal for broader taxonomy, many of the lower categories may come to merit the name of natural genus.

The Higher Taxonomic Categories

Although problems dealing with the lower taxonomic categories are of fundamental importance there are those related to the higher categories that are of equal significance. What taxonomic treatment should the group as a whole receive? The selection of any large taxonomic category, as with the small, should be made on the basis of the largest possible number of essential attributes that the members of the category have in common. Thus in the modern system of classification prepared by Tippo (1941) the terms Trachaeophyta, Pteropsida, Filicinae, and Gymnospermae are used to the exclusion of Spermatophyta and Pteridophyta. Presence of seeds is an attribute which has lost prominence, and the more fundamental attributes expressed in the term Pteropsida have gained. This situation makes it easier to judge the natural affinities in the Fern-Pteridosperm Complex.

However, in the system as Dr. Tippo presents it, there is one point yet to receive attention. If the deletion of the term Spermatophyta is made on the basis that occurrence of seeds as a single attribute lacks enough significance to give it taxonomic precedence over several attributes, perhaps this same single attribute lacks the taxonomic prestige to hold the Pteridosperms among the Gymnosperms. If it does, then the Pteridosperms would be released. Because of distinctive anatomical features, some, in spite of the evidence that they are fern-like, might be regarded as intermediate between Filicinae and Gymnospermae. Others, however, though they bear seeds, should not be excluded by reason of this from the Filicinae, but might better be classified in a natural position, possibly close to the Marattiaceae.

Opposition to this modification would in all likelihood arise out of an objection based on phylogeny. The Marattiaceous Ferns are homosporous whereas it is the popular view that the Pteridosperms along with the other seed plants are heterosporous. There is good evidence to show, however, that the seed plants are homosporous (Thomson, 1927), and it is therefore questionable that the objection has any basis.

In addition to proving homospory in the seed plants, Thomson demonstrates the close relationships between the gymnosperms and the Marattiaceae. He states that: ". . . the Marattia type has attained complete seed orientation. The foot is abortive, a well developed suspensor present, and the leaf of the sporeling is at first embedded in the prothallium and no doubt has acquired some of the absorptive function characteristic of the cotyledon." Van Tiegham showed as stated in Thomson, 1927: ". . . the plane of the wood of the lateral root in the seed plants is parallel with that of its parent root. . . ." Thomson showed that this same parallel orientation is characteristic of certain Marattiaceae, and Weiss (1913) proved it for *Lyginopteris* (*Calymmatotheca*).

The last named example is not the only member of the Fern-Pteridosperm Complex showing Marattiaceous affinity. *Asterotheca parallela* is another (Radforth, 1942) though the relationship here is based on studies of foliage and fructifications. Thomson (1927) suggested that: "When the seed-habit problem is freed from the misconception of the necessity of heterospory it becomes all the more evident that it is in the plexus of early Eusporangiate fossil ferns that we must look for the initial stages of seed-habit organization."

Hence, from the point of view of phylogeny as well as taxonomy it is not unreasonable or unnatural to expect the seed-habit to become established in the Filicinae.

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Studies in the Trigonocarpales. Part II. Taxonomic Problems and a Revision of the Genus Pachytesta

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CONTENTS

I. Some common taxonomic problems 331
II. The Trigonocarpus-Pachytesta complex 336
III. The genus Trigonocarpus 340
IV. The genus Pachytesta 341
V. Description of species 342
P. incrassata 343
P. gigantea 344
P. pusilla 346
P. Noei 348
P. vera 352
P. shorensis 353
P. olivaeformis 354
VI. Other genera of the Trigonocarpales 357
VII. References 360

I. Some Common Taxonomic Problems

Paleozoic seeds are usually found as isolated, detached organs, and the difficulty of determining relationships has long been recognized. In isolated specimens known with structure preserved general relationships to leaf and stem types are generally proposed based on anatomical similarities. Even then such seeds are generally referred to distinct organ genera.

A recurrent problem exists when isolated seeds known only from superficial characters or insufficient structural features are assigned to the same genus as those known with structure well preserved. The basis of this difficulty lies in the extreme variability which may be obtained by a single type of seed depending upon the nature and state of its preservation.

For instance, in the radiospermic seed *Pachytesta vera*, the anatomy of which was described in considerable detail in Part I (Hoskins and Cross, 1946), it is possible to find several preservation forms. Some of these are complete seeds but others may have lost varying amounts of outer tissue. They may be altered, flattened, or variously changed in form. If the surface appears essentially smooth, with longitudinal striations occurring irregularly, it is of the Neuropterocarpus-type shown diagrammatically in figure 49. These striations may be an expression of sclerenchyma strands in the outer tissue, of vascular bundles within the outer fleshy layer, or as shrinkage phenomena.

A second type may be either completely or partially decorticated with its surface marked by numerous more or less strongly developed ridges of the Holcospermum-type as shown in figures 49 and 55. These ridges may vary widely in origin. They may be an expression of the surface of a much ribbed, strong, stony layer either showing through a compressed or shrunken layer of outer fleshy tissue, or the actual surface of the stony layer if all external tissues have been lost; or they may represent the vascular system of the nucellus either as casts or molds of the inner or outer surface of the mature nucellus as in figure 55.

A third type includes specimens which are usually decorticated to some degree, with the surface marked by three prominent major longitudinal ridges occasionally accompanied by a few secondary ridges (figs. 50, 54). These ridges are lateral extensions of the stony layer which are well known in Trigonocarpus. There are occasionally secondary ribs intercalated between them. In a few instances outer layers of tissue may be preserved in such a way as to form wing-like extensions beyond the major ribs, a condition found in forms once called Tripterospermum (fig. 50).

Another type of fossil which may be derived from seeds of Pachytesta is an essentially smooth, rounded or ovoid structure with no further distinctive characters definable. This Carpolithus-type of fossil is often the result of very extensive decortication. Any surface configurations originally present have been lost by imperfect preservation.

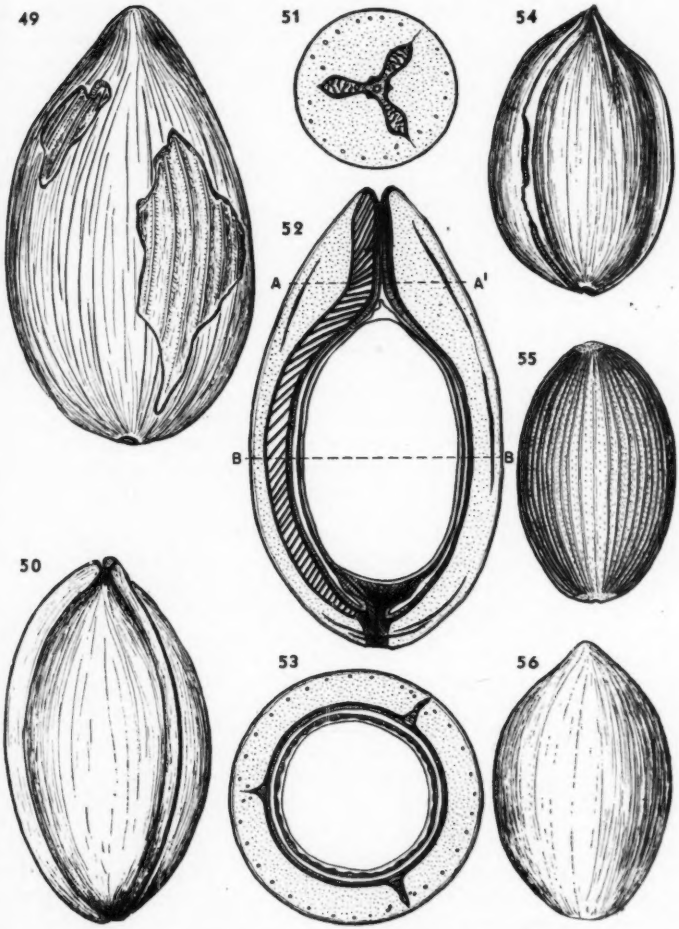
Many of the types of radiospermic seeds referred to the Trigonocarpales, known in some degree of structural detail (figs. 57-65), may be preserved in any one of several ways depending upon conditions of fossilization. Some of these preservation forms are of the same types as those suggested above for Pachytesta. Thus not only may the same seed exhibit several different preservation forms, but also of equal importance, seeds which are quite distinct when known from structure, may be indistinguishable when considered from superficial characteristics alone. A consideration of the genera Trigonocarpus Brongniart and Pachytesta Brongniart may assist in the establishment of a logical approach to problems of this sort.

The genus Trigonocarpus[1] was established by Brongniart (1828) to include radially symmetrical seeds characterized by three longitudinal ribs. He gives no description for the genus but refers to the figures first given by Parkinson (1804, pl. VII, figs. 6, 7, 8). These are incomplete seeds, doubtless casts of the internal face of the integument. These and many species described subsequently were known only from such casts, or from compressions and impressions with little preserved structure.

The first seeds found in which the principal tissues could be studied were in petrifactions and were described by Hooker and Binney (1855) as Trigonocarpus. This appears to be the earliest description of any seed with preserved structure. This material was found in some calcareous nodules of the lower

1 The following footnote by Scott and Maslen (1907, p. 90) is self-explanatory: "Some reason should be given for our use of the form *Trigonocarpus* in this paper instead of *Trigonocarpon*, which was the name used in our preliminary note. The name of this seed has, unfortunately, been spelt differently by different authors. Brongniart himself in his original 'Prodrome' uses *Trigonocarpum*, in his 'Tableau' *Trigonocarpon* is used, while in the memoir on the St. Étienne seeds the genus appears as *Trigonocarpus*. Lindley and Hutton used *Trigonocarpum*, while Williamson adopted Trigonocarpon. Prof. F. W. Oliver, F.R.S., in his recent papers on some of the French seeds uses *Trigonocarpus* and for the sake of uniformity among present-day observers we have adopted the same form."

Figs. 49, 50, 54, 55, and 56.—This series of drawings shows the external apearances possible for a seed of the Pachytesta-type, depending upon the nature and extent of deterioration before or during preservation. Fig. 49 shows the complete seed in external view with two patches of tissue lost, exposing a ribbed structure controlled by the vascular bundles of the integument. Figs. 50 and 54 are the Tripterospermum and



Trigonocarpus-types of fossils showing three main ribs on the surface after the outer fleshy tissue is compressed, shrunken or lost. Fig. 55 represents the Holcospermum-type which shows a number of longitudinal ridges expressing the effect of the vascular system of the nucellus or possibly, too, that surface exposed in the decorticated patches of Fig. 49. Fig. 56 represents a form of the Carpolithus-type which fails to show any distinctive features.

Figs. 51-53.—Figures 51 and 53 are transverse sections of *Pachytesta vera* taken at levels indicated in figure 52. These show the structural organization which may effect the various preservation forms possible. (Reprinted from THE AMERICAN MIDLAND NATURALIST, Vol 36, No. 1, p. 246).

beds in the Lancashire coal field. The assignment of these seeds showing structure to a genus originally proposed by Brongniart (1828) for casts of seeds figured by Parkinson (1804) has led to considerable confusion and uncertainty regarding the characteristics and relationships of these and allied forms.

Not many additional specimens showing structure have been referred to this genus. Williamson (1877) described some additional material as *Trigonocarpon olivaeforme* and states that the Hooker and Binney specimens are of the same type. Subsequently Oliver (1904a, p. 391) pointed out that "The seed described by Williamson under the name *Trigonocarpon olivaeforme*, though slightly larger than the Hooker and Binney specimens, unquestionably belongs to the same affinity." Scott and Maslen reinvestigated the common British species, first calling it *Trigonocarpon olivaeforme* (1906), but in their principal paper (1907), after a critical review of the literature, concluded that the earlier name, *T. Parkinsoni* should be used.

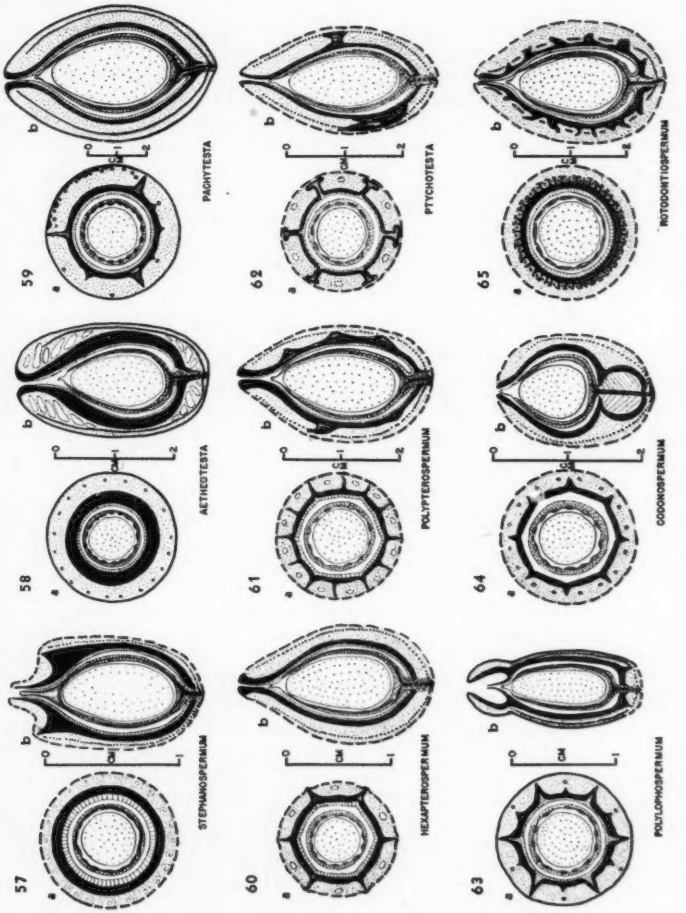
Brongniart (1874a) described a very small seed from St. Étienne as *T. pusillus*. His inadequate description was later augmented by Oliver's study of an additional specimen in Grand'Croix material from the Williamson collection (1904b). Krick (1932) referred a seed from Harrisburg, Illinois, to the same species. The only additional adequately described species of Trigonocarpus is *T. shorensis* founded by Salisbury (1914) on the basis of some well preserved specimens from Shore Littleborough. An examination of the type material of *T. Hookeri* Dawson (1861) and that of the several species of Deevers (1937) indicates that these specimens lack sufficient structure to corroborate their present designations on the basis of their fundamental tissues.

A survey of the literature demonstrates the difficulty of correlating these seeds known from structure with those known from superficial or inadequate structural features only. This difficulty is increased when seeds described and classified from external characters are later found to possess structure. An example of this difficulty may be drawn from the work of Reed (1939) who studied the anatomy of a seed collected at Polk's Patch, near Boonville, Indiana, by the late Professor Noé. This specimen from the Allegheny Formation was figured as Trigonocarpus by Chamberlain (1935, p. 26, fig. 23). The original identification of this seed as Trigonocarpus was logical on the basis of its external features (fig. 67). Its structure, however, proved the error of its original classification for Dr. Reed's investigations of the anatomy of this seed showed that its structure was not that described for the genus Trigonocarpus but rather that reported for Pachytesta. This example emphasizes the constant dangers attendant upon using the same generic designation for isolated specimens established upon external features as for those with structure preserved. for in most instances the identification of seeds based upon external characteristics cannot be corroborated because of the lack of adequate preservation of anatomical features.

Brongniart (1874a) encountered such a difficulty in his investigation of Pachytesta. Certain of the seeds placed in that genus on the basis of their anatomy were similar to others which Grand 'Eury had identified, according to Brongniart, as *Rhabdocarpus giganteus*. Brongniart stated that the study of their structure showed that they had nothing in common with the genus

Rhabdocarpus, the longitudinal striations which they showed on their surface not having the same origin.

It thus appears that as a practical necessity those genera of the Trigonocarpales which were originally described from structure should be restricted to include those forms the anatomy of which is adequate for that determination.



Figs. 57-65.—Distinctive generic characteristics of nine genera of seeds which have been referred to the Trigonocarpales and are known from structure are shown in median transverse and longitudinal diagrammatic reconstructions. Broken and dotted lines indicate tissues the full extent of which is uncertain.

Genera based on external features should not be extended to include seeds whose structure is inadequate for critical identification.

This point of view has been discussed by many of those whose work has brought to them the problem of correlation. Seward (1917) raises the issue many times. In discussing the seeds of Neuropteris, (p. 115) he wrote: "With a view to avoid the danger of incorrectly identifying petrified specimens and impressions that cannot be proved to belong to the same generic type, I have suggested the restriction of the name *Rhabdocarpus* to seeds that do not furnish evidence as to internal structure, and the employment of the designation *Rhabdospermum* for seeds that conform to those described by Brongniart as *Rhabdocarpus*." Kidston (1892, p. 8), in discussing a seed which he thought might be allied to Pachytesta, added, "I do not think we are justified in placing mere impressions of plants in genera, whose distinctive characters are derived from their internal organization, unless there is *conclusive evidence*[2] to show their identity." Arber (1914, p. 82) stated "At the present time there is considerable confusion as to the limits of the generic terms in common use. This arises partly . . . because of the extremely unfortunate practice of including impressions in genera founded on structural material, or *vice versa*, without at the same time affording *satisfactory proof*[2] of the correlation of the impression with the petrifaction or *vice versa*. This is quite unjustifiable."

It is obviously desirable to effect every possible correlation between isolated units of fossil material regardless of method of preservation. The question arises, however, as to what is 'satisfactory proof', or 'conclusive evidence' for such correlation. It is perhaps better to minimize this difficulty by the suggested restriction of the limits of the genus. This in no way limits the suggestion of, or even certainty of affiliation. It merely reflects the extreme difficulty of being *sufficiently certain*.

II. The Trigonocarpus-Pachytesta Complex

If the genus Trigonocarpus, therefore, is to be restricted to designate certain seeds known from external characteristics, it is necessary to determine the proper disposition of those specimens described from structure and included in the genus. As will be demonstrated below, it is not possible to exclude the species of the genus Pachytesta from a consideration of the species of Trigonocarpus. A review of the fundamental structure of *Trigonocarpus Parkinsoni* Brongn., *T. pusillus Brongn.* and *T. shorensis* Salisbury, and of *Pachytesta gigantea* Brongniart ex Renault, *P. incrassata* Brongn., *P. vera* Hoskins and Cross and the specimen described by Reed (1939) as *P. gigantea*, which is shown below to be a new species, shows an intergrading series. It appears reasonable to include all of these forms within a single genus. A brief survey will support this conclusion.

All of these species are radiospermic. In all the nucellus is entirely free from the integument and more or less pedicellate. All have a vascular system arising from a single strand which enters the base of the seed, one series of

2 The italics are our own.

branching forming an integumentary system, a second series forming a nucellar system. All have a single complex integument, some, probably all, with an inner fleshy layer, all with a stony layer bounded externally by a zone of parenchyma. These characteristics, of course, are those generally attributed as well to all members of the Trigonocarpales heretofore described from structure.

Further, these species generally agree in form. They are more or less ovoid, being circular in transverse section and oval or slightly attenuated in longitudinal view. In this respect they are quite similar to the seeds of most of the genera of the Trigonocarpales except Stephanospermum and Polylophospermum and possibly others which appear to be angular rather than circular in transverse section, a condition due possibly to incomplete preservation of the outer tissues of the integument. In longitudinal view probably only Stephanospermum and Polylophospermum are distinctly different. These two are characterized by perimicropylar collars of tissue expressing the extension of the stony layer of the integument. The latter genus also has a peribasal flange not common to the other genera.

The species of Pachytesta and Trigonocarpus all agree in general structure of the integument. All possess a conspicuous stony layer. This layer is divided into 3 essentially equal valves (appearing as arcs in transverse section) by the regular occurrence of 3 zones of specially organized tissue. Sutures or commissures develop at these zones, especially toward the upper part of the seed, and extend radially not only through the stony layer but more or less through the entire integument. These may well have been dehiscence lines of a tripartite seed.

The stony layer may extend radially into the parenchymatous tissue of the integument at these three areas forming 3 more or less conspicuous primary ribs. Smaller secondary ribs may occur between the primary ribs. These are best developed at the base and/or the apex. No commissures or lacunar tissue occurs at the position of any secondary rib. This tripartite character of the seed with commissures occurring in the 3 primary ribs is not a characteristic of any of the other genera of the Trigonocarpales known from structure.

A comparison of the fundamental tissues of the species of Trigonocarpus and Pachytesta known from structure emphasizes the absence of any adequate generic distinction between them. For instance, the outer zone of the integument may be entirely free of mechanical tissue (*Pachytesta vera*), or there may be irregular plates or zones of fibrous tissue (*Trigonocarpus shorensis*), or the outer zone may be composed of mechanical tissue which forms an outer cylinder of varying degrees of thickness, both in different species and at different levels in the same specimen (*Pachytesta gigantea, P. incrassata*). In the outer tissue of *Trigonocarpus Parkinsoni,* Scott and Maslen record a thin hypodermis near the periphery and the *'cellules rayonnantes'* as described by Brongniart for *T. pusillus* may represent a similar structure.

The parenchyma of the integument varies considerably from species to species and in the same specimen. It is described as tortuous and sinuous by Renault for *Pachytesta incrassata* and dense and less tortuous for *P. gigantea.* Reed's specimen appears to be transitional between this condition and the typical parenchyma of *P. vera.* In *Trigonocarpus shorensis* and *T. Parkinsoni* the outer portion of the fleshy layer is loosely organized and possesses variable

lacunar areas. In *Pachytesta vera* there appear to be no definable lacunae although there are areas of parenchyma which are very loosely organized.

The stony layer of the integument may have radial extensions (ribs) scarcely evident as in *Trigonocarpus pusillus,* or more strongly developed as in *Pachytesta gigantea,* or they may be very prominent as in *Trigonocarpus Parkinsoni.* These ribs are usually more strongly developed toward the apex. Secondary ribs seemed to have been a constant feature throughout the length of the seed in *T. Parkinsoni,* in *T. shorensis* they occur only at the base, whereas in *Pachytesta vera* they occur only at the top. Because this situation may differ at different levels in the seed, the similarity of transverse sections through the center of the seed of *Trigonocarpus shorensis* (Salisbury, 1914, pl. 4, fig. 1) and *Pachytesta vera* (Hoskins and Cross, 1946, fig. 5) is striking. As far as can be determined no secondary ribs are present in *Trigonocarpus pusillus, Pachytesta gigantea* and *P. incrassata.*

There is considerable variation in the proportional length of the micropyle to the overall length of the seed. The following are fairly close approximations: *Trigonocarpus pusillus,* micropyle one-seventh total length of 6.5-7.5 mm.; *T. shorensis,* one-fourth total length of 4.5 cm.; *T. Parkinsoni,* one-half total length of 4 cm.; *Pachytesta gigantea* of Reed (1939), one-seventh total length of 6 cm.; *P. vera,* one-fourth the total length of 7 cm.; *P. gigantea,* one-fifth the total length of 8-9 cm.; and *P. incrassata,* one-fifth the total length of 10-11 cm.

Thus it can be seen that no generic distinction can be based on the nature of the integument alone. While the various species demonstrate considerable latitude in the organization of the integument, this cannot be correlated with other specific differences.

The structure and organization of the nucellus of these species is remarkably similar with only minor specific differences recorded. The striking feature which has been commonly recorded for Pachytesta, also suggested by Renault (1896) for *Trigonocarpus pusillus,* namely, the peculiar attachment of the nucellus to the surrounding integument by a number of intermeshing grooves and plates as described by Brongniart (1874, 1881) and Renault (1896) and elaborated by Oliver (1904b) was shown by us (1946) to be a misinterpretation. Thus a major distinction of long standing between these two genera is eliminated.

The vascular organization of the integument presents at first glance the greatest difficulty in assembling these species into a single genus. While all species show essentially the same picture as to the origin of the integumentary vascular system, there is great variation in the accounts given of the total number of bundles present in transverse sections of the seed and as to their position within the integument. The variation recorded ranges from that given for *Trigonocarpus Parkinsoni* where two bundles are reported to occur between each pair of major ribs to *Pachytesta gigantea* and *P. incrassata* where the number of bundles is indefinite but large, and supposedly arranged in two concentric rows forming the "double" vascular system of the integument. In Part I of this paper (1946) we discussed the vascular system of the integument of these two species and concluded on apparently ample grounds that they do

not possess a double system but are quite comparable to that described for *P. vera.*

The earlier descriptions of *T. pusillus* by Brongniart (1881) and Renault (1896) and later by Oliver (1904b) omitted consideration of the integumentary vascular system as little tissue was present in their specimens exterior to the stony layer. The specimen described by Krick (1932) as *T. pusillus* does not appear to belong to this genus. The organization of the vascular tissue in the outer fleshy layer requires additional investigation of specimens where the outer tissues of the integument are unquestionably preserved.

Trigonocarpus Parkinsoni, according to Scott and Maslen (1907), possesses six or possibly nine bundles by their own account. The position of the bundles appears to be opposite those secondary ribs which are adjacent to primary ribs. The presence of bundles opposite the middle of the three secondary ribs in each arc of the outer parenchyma could not be finally determined. The lack of preservation of most of the tissue external to the stony layer accounts for the difficulties of final determination. Salisbury (1914), on the basis of additional observations, believed the number to be six. This species stands apart, however, in the fact that the bundles are quite deeply placed in the outer parenchyma (also in the thickness of the stony layer and prominence and persistence of the secondary ribs), rather than peripherally placed as in the other species.

Salisbury's account of *T. shorensis* (1914) reports the presence of two vascular bundles in each arc of the outer fleshy layer. These bundles are situated midway between a major and a minor rib. The most important difference in the vascular organization from *T. Parkinsoni* in his opinion is the peripheral position of the bundles in *T. shorensis.*

Dr. Reed's specimens of Pachytesta (1939) have a single peripheral series of bundles which she states number 20 or more. As nearly as we can determine from an examination of a portion of her material and her illustrations it is probable that the number is between 18 and 27. In comparison with the figures of *P. gigantea* by Brongniart and Renault, this number is small.

We have shown (1946) that in *P. vera* a single peripheral integumentary vascular system was present with the bundles adjacent to the major ribs being more deeply placed than the others. In the central area of the seed the number of bundles is about 36, more than in Reed's specimen, less than in *P. gigantea* and *P. incrassata.* In *P. vera* there is some evidence that the bundles are definite in number, in multiples of 3, but in the majority of sections this cannot be demonstrated, the number being approximate only.

To summarize, it appears that the vascular bundles of the integument are few (6), definite in number, peripherally placed (*T. shorensis*); same number or more(?), (6 or 9?), deeply placed in the parenchyma (*T, Parkinsoni*); more numerous (18-27), peripherally placed (*Pachytesta gigantea* of Reed, not Brongniart ex Renault); number slightly larger (18-36), some evidence of definite number, peripherally placed (*P. vera*); or finally, number large, (45?) indefinite (*P. gigantea, P. incrassata*).

Here, then, we have series of variations which, when considered as a whole are insufficient to distinguish between the genera Trigonocarpus and Pachytesta. It is interesting to note that individual variations of one kind tend to

balance or nullify the variations in another direction thus tending to unify the group rather than to emphasize differences. We believe that all of these species fall logically into a single genus.

III. The Genus Trigonocarpus

The need is obvious for the retention of the name Trigonocarpus as the generic designation for fossil seeds similar to and identifiable with those which were first illustrated by Parkinson (1804, pl. 7, figs. 6, 7, 8) and reprinted here in figure 66. Although Brongniart named these seeds without describing them (1828) taxonomic rules provide for the priority of the names for fossil plants if adequately figured in publications prior to 1908. A vast number of specimens, now grouped in a great number of species, have been assigned to the genus. The majority of these seeds can provide no further identifying features than are now recorded. They may actually be derived from a number of genera of plants living in the Paleozoic Era, but are inadequately preserved to be placed in more natural groups. A restudy would likely disclose

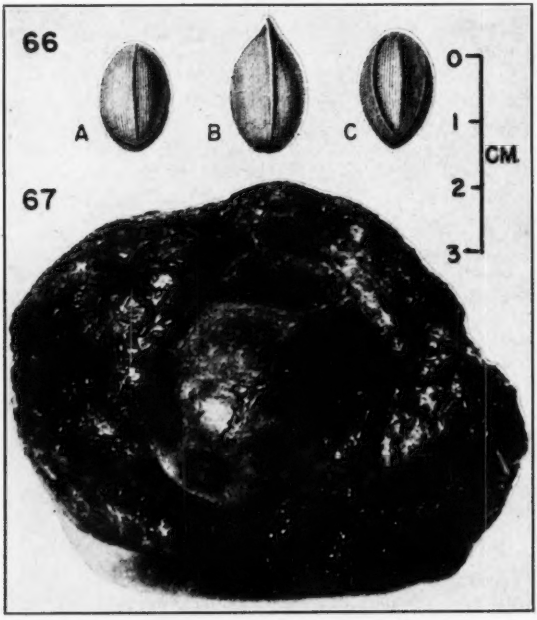


Fig. 66, A, B, C.—Reproduction of figures 6, 7, and 8, respectively, of Pl. 7, from Parkinson's *Organic Remains*, Vol. I, 1804, referred to by Brongniart as illustrative of *Trigonocarpus Parkinsoni*.

Fig. 67.—*Pachytesta Noei*, holotype, originally figured as Trigonocarpus in Chamberlain, *Gymnosperms, Structure and Evolution* (1935, fig. 23).

the inclusion of many on inadequate proof. Perhaps even more general categories will be required to receive some of them. But for the great number of this type which are surely identified, the only legitimate name to receive them is Trigonocarpus. The synonymy and description of the genus follow.

TRIGONOCARPUS Brongniart.

1828 *Trigonocarpum* Brongniart, Prodrome, p. 137.
1804 (No name) Parkinson, Org. Rem. **1**:458, pl. 7, figs. 6-8.
1820 *Carpolites* Sternberg Vers. ein. geogn.-bot. Darst. d. Flora d. Vorwelt. Heft I, pl. 7, figs. 14a, 14c, 16.
1826 *Palmacites* Sternberg, ibid. Heft IV, p. 35, pl. 55, figs. 6, 7; pl. 58, fig. 3.
1874 *Trigonocarpus* Brongniart, Compt. rend. **79**(7):431, pro parte.
1877 *Polypterocarpus* Grand 'Eury, Mem. Acad. Sci. Inst. France **24**(1):185, pro parte, pl. 15, figs. 9, 11; pl. 16, figs. 2-4.
1877 *Carpolithus* L. in Grand 'Eury, ibid. **24**(1): 187, pro parte, pl. 15, fig. 9.
1896 *Tripterospermum* Brongn., In Renault, Flore Fos., Gîtes Minér. France, p. 404.
1914 *Schizospermum* Arber, Ann. Bot. **28**:86-87, 103, pl. 8, figs. 48-50.
1914 *Radiospermum* Arber, ibid. **28**:92-93, 101-103, pro parte, pl. 7, figs. 32, 38-41; pl. 8, figs. 44-45.
1914 *Pterospermum* Arber, ibid. **28**:93-94, 104, pl. 8, figs. 51-52.

Radially symmetrical seeds which may have been more or less flattened in fossilization; preserved as casts, compressions or impressions.

Elliptical to ovoid or obovoid in form or outline, with the tip more or less attenuated and the base blunt or rounded, often with central pit.

Surface of seeds smooth with three more or less prominent (major) longitudinal ribs determinable, and secondary multiples present in some number and degree of development or absent; usually the ribs extend more or less from base to apex and are frequently more prominent above, occasionally being attenuated apically, and less often laterally extended in the form of flanges or wings.

These seeds are identifiable by superficial features only, because their internal structure is insufficiently preserved. They may exhibit varying degrees of decortication or tissue deformation (compression) acquired before or during fossilization.

IV. The Genus Pachytesta

As Trigonocarpus is thus occupied another name must be used for the group of seeds with structure preserved and formerly assigned to the genus Trigonocarpus, as well as for those assigned to Pachytesta, which we have shown above to be indistinguishable and hence belong to the same genus.

The first generic name to be used for any radiospermic seed based primarily on its structural characteristics was Pachytesta. Only the Hooker and Binney material was known from its structure earlier than the specimens described by Brongniart in 1874. Brongniart's brief description was augmented by the superb plates in the posthumous memorial publication (1881) and by Renault's later review (1896). The only other generic name which perhaps should be considered as the proper designation for this group of seeds is Tripterospermum which is, we believe, not acceptable. In the first place the original

description of this genus followed that of Pachytesta in Brongniart's 1874 report (1874a, pp. 432-433). Furthermore its validity was questioned by Renault and Oliver and it was considered as synonymous with Trigonocarpus by Scott and Maslen. We agree with their argument and conclusions.

We propose, then, by the extension of the definition of the genus Pachytesta to include those seeds known from structure which have heretofore been described as Trigonocarpus and Pachytesta. The synonymy and emended description follow.

Pachytesta (Brongniart) Hoskins and Cross, emend.

1874 *Pachytesta* Brongniart, Compt. rend. Paris **79**(7):430-431.
1855 *Trigonocarpon* Brongn., in Hooker and Binney, Phil. Trans. Roy. Soc. London **145**:149-154, pl. 4.
1874 *Trigonocarpus* Brongn.., in Brongniart, Compt. rend. Paris **79**(7):431-432, pro parte.
1874 *Tripterospermum* Brongniart, Compt. rend. Paris **79**(7):432-433.
1877 *Trigonocarpon* Brongn., in Williamson, Phil. Trans. Roy. Soc. London B, **167**: 248-254.
1907 *Trigonocarpus* Brongn., in Scott and Maslen, Ann. Bot. **21**:96-124.
1914 *Trigonocarpus* Brongn., in Salisbury, Ann. Bot. **28**:39-62.
1939 *Pachytesta* Brongn., in Reed, Bot. Gaz. **100**:776-782.
1946 *Pachytesta* Brongn., in Hoskins and Cross, Amer. Midl. Nat. **36**(1):207-251.

Seeds radially symmetrical, ellipsoidal to ovoid or obovoid, with apical end rounded or more or less attenuated, with structure sufficiently preserved to show the following morphological features:

A stalked nucellus, free from the integument.

A single vascular supply branching near the base of the seed to form an integumentary vascular system and in the base of the nucellus to form a nucellar vascular system.

A multiple-layered integument, usually consisting of a thin parenchymatous inner fleshy layer, a sclerotic or stony layer, and an outer fleshy layer which is often heterogeneous, with varying amounts and arrangements of sclerotic tissue.

An integument more or less divided into 3 approximately equal valves by longitudinal commissures which are generally bounded by radial extensions from the sclerotic layer. Between these commissured radial sclerotic extensions (primary ribs) non-commissured secondary ribs may occur.

The structural characteristics of this genus are discussed in considerable detail in Part I and need not be reviewed here.

V. Description of Species

The synonymies and descriptions of seven species follow. A reexamination of the type material as prepared by the authors of *Trigonocarpum Hookeri* Dawson (1861) and of the several species of Trigonocarpus described by Deevers (1937) indicates an absence of the critical features necessary to warrant their transfer to Pachytesta at this time.

PACHYTESTA INCRASSATA Brongniart, Ann. Sci. nat. Bot., 5. sér., 20: pl. 22, fig. 4 (above), fig. 5(?). 1874.

1881 *Pachytesta incrassata* Brongniart, Recherches graines fos. silic. Paris, pl. B, fig. 4 (above), fig. 5(?); pl. 17, fig. 6; pl. 19, figs. 1, 2; pl. 20, figs. 1-3.
1896 *Pachytesta incrassata* Brongniart, in Renault, Flore fos. Gîtes Minér. France, pp. 390-391.

Organization.—Seeds very large, measuring 10-11 cm. long by 5-6 cm. in diameter, radially symmetrical, ellipsoidal, with extremities attenuated and rounded. Nucellus stalked and entirely free from the integument, occupying about three-fourths the entire length of seed. A single vascular bundle enters the base of the seed and branches to supply both the integument and nucellus.

Integument.—Approximately 8 mm. thick in central portion of seed, expanding somewhat at base and tip to about 12 mm. Composed of 4 principal regions, 1) an outer layer of stony tissue, 4-5 cells wide, appearing to be nearly isodiametric but slightly elongated radially, with very thick walls. These cells are slightly smaller than those of 2) the main fleshy layer which occupies most of the integument. The fleshy tissue is composed principally of prismatic parenchyma cells. Near the base and apex, and elsewhere toward the outside and inside, the cells are often somewhat elongated and sinuous forming a compact fibrous layer. Internal to this is 3) another zone of sclerotic tissue which differs from the outermost layer in having thinner-walled stone cells, slightly elongated longitudinally and filled with dense resinous contents, and 4) a delicate inner fleshy layer which was surely present in natural condition, is represented only by a strong cuticle facing the nucellus. This cuticle is usually pulled away and follows the outline of the shrunken nucellus. The integument is divided into 3 valves by longitudinal commissures which are located in zones of sclerotic tissue (ribs) which appear to have developed radially from the inner stony layer. Occasionally at these sutures, slight inward development of the stony layer is evident. The nature of the outer epidermis is unknown.

Nucellus.—Ellipsoidal, borne on a prominent stalk about 2 mm. high and 5 mm. in diameter, surrounded by a strongly reflexed collar composed of a mass of sinuous cells of the strong chalazal disc. The summit of the nucellus is somewhat conical and is surmounted by a prominent beak which probably was inserted in the lower part of the micropylar canal. This nucellar beak is lined with at least one layer of modified cells. Tissue of the nucellus is reduced to a well-defined epidermis of large cells filled with dark contents, and with a conspicuous cuticle, surrounding a thin-walled parenchyma of a few cells in thickness except at apical end. There it is reduced and encloses an unspecialized pollen chamber. A vascular system traverses the peripheral remnant of the nucellus.

Vascular System.—A single large vascular strand enters the base of the seed and branches in a close series to form numerous bundles (18 or more per arc of the integument) which traverse the outer zone of the fleshy layer in essentially a single row, although bundles placed deeper in the tissue may occasionally be present especially adjacent to commissures and toward the base of the seed. The main strand continues to the base of the nucellus where

it is completely dispersed in a close series of branches which pass outward and upward longitudinally forming discrete bundles and disappearing at the level of the top of the megaspore.

Spores and Pollen Grains.—One large functional megaspore, represented only by its thick wall, nearly filling the nucellus in petrified state. Over 100 pollen grains (and spores) of fairly uniform type have been found in the pollen chamber and nucellus beak. These appear to be 35-40μ in longest diameter and are probably multicellular.

Locality and Horizon.—Stephanian (Grand'Croix); silicified magmas near Saint Étienne.

Material.—Several silicified specimens.

Lectotypes.—Specimens figured by Brongniart (1881), pl. 17, fig. 6; pl. 19, figs. 1, 2; pl. 20, figs. 1-3.

The seeds of this species are the largest known for the genus. They have been clearly figured by Brongniart (1881) and a type description was given by Renault (1896). There has been some misinterpretation of the exact nature of the tissues of the inner part of the integument and the outer part of the nucellus, and in the nature of the branching of the vascular bundles from the main strand at the base of the seed and their disposition within the integument. We have shown in Part I (1946) that the nucellus was not united to the integument by a system of intermeshing longitudinal grooves and ridges, and that the disposition of the integumentary vascular system was fundamentally that of a single row of peripheral vascular bundles and not a "double" system of two rows.

PACHYTESTA GIGANTEA Brongniart ex Renault, Flore fos. Gîtes Minér. France, pp. 392-393. 1896.

1874 *Pachytesta gigantea*(?) Brongniart, Ann. Sci. nat. Bot., 5. sér., **20**: pl. 22, fig. 4 (below).
1877 *Pachytesta gigantea* Brongniart, in Grand 'Eury, Mém. Acad. Sci. Inst. France **24**(1):203, line 20 to base of page; not *P. gigantea*, p. 204, pl. 16, fig. 5.
1881 *Pachytesta gigantea* Brongniart, Recherches graines fos. silic. Paris, pp. 23-24, pl. 17, figs. 1, 3-5, 7-8; pl. 18, figs. 1-2; pl. 21, figs. 1-6.
1893 *Pachytesta gigantea* Brongniart, in Renault, Flore fos. Gîtes Minér. France, pl. 83, figs. 4-5; pl. 84, figs. 1-2.

Organization.—Seeds very large, 8-9 cm. long by 3-4 cm. in diameter, radially symmetrical, ellipsoidal, somewhat prolonged at top into a blunt beak. Nucellus short stalked and free from integument, occupying slightly more than three-fourths the entire length of seed. A single vascular bundle enters the base of the seed and supplies both integument and nucellus.

Integument.—Approximately 6 mm. thick in central portion of seeds, generally thinner throughout and not as markedly expanded at base as in *P. incrassata*. The histology of the integument is essentially similar to that of *P. incrassata* except that the outer stony layer is slightly thinner. The cells of the inner stony layer are clearly elongated.

Nucellus.—The nucellus stalk is shorter (about 1 mm.) and appears to be slightly stouter than in *P. incrassata*. The reflexed collar surrounding the stalk is thicker as is the strong chalazal disc. The other characteristics of the

nucellus are similar to those of *P. incrassata*. No connections exist between the integument and nucellus as were once suggested to explain certain shrinkage phenomena of the outer tissues of the nucellus and the inner epidermis of the integument.

Vascular System.—A single large vascular strand, in a close series of branches, gives off numerous integumentary bundles and continues into the base of the nucellus where it divides completely, forming the nucellar vascular system. Both of these systems are disposed peripherally in their respective tissues (integument and nucellus), as in *P. incrassata*, in a single row, with an occasional bundle being more centrally orientated in the integument. The elements appear to be scalariform.

Spores and Pollen Grains.—Only the functional megaspore is represented. Pollen grains have been recorded (Renault, 1896) but are not adequately described nor figured.

Locality and Horizon.—Stephanian (Grand'Croix), silicified magmas near Saint Étienne.

Material.—Several silicified specimens.

Lectotypes.—Specimens figured by Brongniart (1881), pl. 17, figs. 1, 3-5, 7-8; pl. 18, figs. 1-2; pl. 21, figs. 1-6.

It is evident from the above description that this species is to be closely compared with *P. incrassata*. The distinguishing features appear to be the smaller size, the thinner integument at base and apex, the shorter and thicker nucellus stalk, and the thicker chalazal disc and reflexed collar surrounding the stalk at the base.

It is quite difficult to determine the proper name and authority for this species. It appears that Grand'Eury first used the specific name as early as 1872, in a manuscript submitted for publication (which remained for several years unpublished), to describe some petrified seeds which he had identified as *Rhabdocarpus giganteus* on the basis of superficial characteristics. This material was a part of his collection of silicified petrifactions from Grand'-Croix. Brongniart says in his description of Pachytesta (1874a) that these seeds from St. Étienne, designated by Grand'Eury as *Rhabdocarpus giganteus*, have a different structure than that known for the genus Rhabdocarpus. He proceeded, therefore, to describe them on the basis of their anatomy as *Pachytesta*. No specific names are used by Brongniart in his description of the genus, but in the plates which appeared with the reprinted text of his description in volume 20 of the *Annales des Sciences Naturelles, Botanique* (1874b), he refers the lower drawing in figure 4, plate 22, to *P. incrassata* (?) or *P. gigantea*, inferring uncertainty as to specific identification.

Grand 'Eury's comprehensive report on these, and other fossils, finally appeared as a separate volume three years later (1877). This surely is the report referred to by Brongniart in his "Rapport" before the Academy (1872) and in his references to Grand 'Eury's work (1874a, 1874b). Grand 'Eury (1877) gave a very brief description of the anatomy of Pachytesta and stated (p. 203, lines 20-22) that Brongniart would make known the organization. Actually Brongniart *had already* made known the organization of the genus in 1874, but it is not clear which of the 2 species, *P. gigantea* or *P. incrassata*, if either one alone, was referred to at that time, for both were mentioned in

the legends to the plates. Grand 'Eury's description of *P. gigantea*, page 204, and his figure 5, plate 16, are based solely on external and superficial characteristics of several compressions showing the features of the outer tissue (epitesta) and an outline of an enclosed central body.[3] The seeds referred to are from a number of coals and carbonaceous shales and no mention is made of the petrified material from Grand'Croix. Therefore such a diagnosis is incompatible with the earlier description and illustration by Brongniart (1874) for the genus Pachytesta, later augmented by the plates in 1881. Grand'Eury's identifications of these specimens as Pachytesta, a genus based on structure, could only have been inferred, not proved, and they may have included a number of unrelated forms. Therefore, since Brongniart's name, *P. gigantea* appeared first, i.e., *before the publication* of Grand 'Eury's earlier work, it cannot be considered to have been "transferred" from *Rhabdocarpus giganteus*, which was then as yet (1874) unpublished, nor can it be considered to apply to forms not identifiable from structure. Grand 'Eury's designation of some compressed specimens not showing structures necessary for comparison, therefore, is invalid, both by the use of a preoccupied name and by reference to a genus to which it could not be compared structurally. The late publication date of Grand 'Eury's work thus affords the official premise for invalidating his authorship of the name according to the rules of botanical nomenclature. Otherwise it would have been desirable to have initiated measures necessary to conserve such a well established name.

Brongniart's first references to this species (*P. gigantea*) are too inadequate to be considered as valid in the light of modern rules of nomenclature, but since the first description and illustration were later thoroughly clarified and augmented by his plates (1881), and the species more completely described by Renault (1896), the selection of the name and authority as *P. gigantea* Brongniart ex Renault appears to be the most justifiable and logical.

Pachytesta pusilla (Brongniart) Hoskins and Cross, comb. nov.

1874 *Trigonocarpus pusillus* Brongniart, Compt. rend. Paris **79**(7):431-432.
1874 *Trigonocarpus pusillus* Brongniart, Ann. Sci. nat. Bot., 5. sér., **20**: pl. 22, figs. 1-3.
1904 *Trigonocarpus pusillus Brongniart*, in Oliver, New Phytol. **3**:96-100, pl. 2, figs. 1-3.

Organization.—Very small, radially symmetrical, ovoid seeds (stony layer of integument slightly triangular in transverse section), 6.5 mm. long by 4.5 mm. in diameter, rounded at base, apical organization incompletely known. Nucellus ovoid, short stalked and free from the integument, occupying about five-sixths of the entire length of seed. A single vascular supply branches in the base of the nucellus in such a way as to form the nucellar vascular system. The vascular organization of the integument is unknown, probably due to incomplete preservation of external tissues.

3 "Les terrains houillers . . . renferment les graines . . . , elliptiques, oblongues dans l'ensemble, . . . réduites à l'épitesta marqué en long de stries parallèles et présentant un countour intérieur de semence beaucoup plus petite."

Integument.—Very thin and dense, composed of compact tissue throughout except at the periphery where two layers of radiating cells are differentiated. Nothing is known of the outer epidermis, and the outer fleshy layer present in other species appears to have been lost prior to fossilization, absent or greatly modified. The inner fleshy layer is unknown except for the inner epidermis and cuticle which are shown (Oliver, 1904b, figs. 1-3) to have been stripped away from the inside of the integument, toward the top of the seed, and collapsed or shrunken around the upper end of the nucellus.

Nucellus.—The nucellus occupies almost the whole cavity of the seed in preserved condition and appears slightly angled in tranverse section corresponding to the outline of the integument. The base is blunt and borne on a short thick stalk which expands to form the chalazal disc. The wall of the nucellus, composed of thin parenchyma, is traversed by the small nucellar bundles and is bounded by a thin epidermis. A conspicuous pollen chamber is present at the apex.

Vascular System.—A single strong vascular strand enters the base of the seed, traverses the basal tissues to the base of the chalaza and disperses to form discrete bundles extending upward in the peripheral zone of the nucellus to the base of the pollen chamber.

Spores and Pollen Grains.—A single functional megaspore, represented by a heavy membrane only, fills the nucellar cavity. A number of pollen grains have been recorded as being present in the pollen chamber, but the exact nature of these is unknown.

Locality and Horizon.—Stephanian (Grand'Croix), silicified magmas near St. Étienne.

Material.—Several silicified petrifactions.

Lectotype.—Specimen figured by Brongniart (1874b), pl. 22, figs. 1-3.

Brongniart's description (1874, 1881) of this species, while in brief and general terms, nevertheless included the primary characteristics of the genus, namely, the division of the integument into three arcs (in transverse section) by the occurrence of three commissures or ribs. Oliver's consideration (1904b) still left much detailed information to be desired. Krick (1932) in describing a seed from Harrisburg, Illinois, as *Trigonocarpus pusillus,* gave needed information concerning size, nature of the integument and its vascular system. A reinvestigation of her preparations failed, however, to provide evidence that the integument possessed 3 ribs or commissures, or that vascular bundles occurred in the nucellus or integument. The organization of the integument which is preserved in excellent and complete detail in some areas, while suggestive of certain other seeds, differs in many respects from known species of Pachytesta. It thus appears that as the primary requirements for inclusion within the genus are apparently lacking, its proper designation must await further study.

Oliver's interpretation of the organization of the external tissues of the nucellus (1904b), and especially that of the epidermis (described and figured at "E", fig. 1, pl. 2, as belonging to the nucellus) of the inner surface of the integument, is doubtless in error as has been shown (Part I). No description of the pollen grains is given other than that they are "pluricellular" (Oliver, 1940b, p. 97).

Pachytesta Noei Hoskins and Cross, spec. nov.

1939 *Pachytesta gigantea* Ad. Br., in Reed, Bot. Gaz. **100**:776-779, figs. 11-15, not *Pachytesta gigantea*, in Brongniart 1874b, 1881; Renault and Zeiller, 1888, 1890; or Renault 1893, 1896.

Organization.—Seeds large, radially symmetrical, elongate-ellipsoidal, about 6 cm. long by 2.5 cm. in maximum diameter; rounded at base, form of apex not known. Nucellus entirely free from integument, pedicellate, occupying about four-fifths of the entire length of seed. Vascular system present in both integument and nucellus but organization at base of seed unknown.

Integument.—Average thickness in central region 2 mm., increasing in thickness toward apex (4.75 mm. at level of micropyle) and at base (3 mm. at level of chalazal disc). Composed of five principal zones: 1) a thin peripheral parenchymatous layer of 5-9 cells (average of 7 in central region), each 25-40μ in diameter, with walls 3-6μ thick, increasing in number toward the tip. This tissue grades insensibly inward into 2) a layer of strong tissue, the outer 5-7 rows of cells of which are the same size as the peripheral cells but with much thickened walls. These cells become progressively larger inward to the main zone of this peripheral stony layer which is very irregular in thickness, composed of 6-15 rows of isodiametric cells which vary in size from 40-105μ (the majority of cells are about 60μ), with walls about 18μ thick (varying from 8-22μ). Internal to this and occupying a larger portion of the integument is 3) a parenchymatous layer of 20-30 firm, essentially isodiametric cells, extremely variable in size (from 20-100μ), the majority being about 50μ, with walls varying from 6-10μ thick. This tissue is very compact with only an occasional intercellular space. The thicker walled cells of this layer are irregularly distributed throughout the tissue, both aggregated into groups and occurring singly. This zone is sharply delimited internally by 4) an inner stony layer quite different from the peripheral sclerotic layer, but essentially similar of the stony layer of *P. vera* and *P. shorensis*. It consists of narrow, vertically elongated cells with blunt ends which appear to be 20 to 30μ wide and up to 200μ or more in length, somewhat sinuous and slightly intertwined. Entire layer about 0.2 mm. thick and composed of 10-13 rows of cells (occasionally as few as 7 rows) and appears to be distinctly separate from the surrounding fleshy layer, a separation line often being present, but occasionally a few cells are directed outward into the parenchyma. This layer is further characterized by the accumulation of dense contents within the cells. Normally this tissue is found facing the nucellus cavity but occasional remnants mark the former presence of 5) an inner fleshy layer of delicate parenchyma. This innermost layer of the integument is represented in the central part of the seed by its strong epidermis (fig. 70), which is usually pulled away and follows somewhat the contour of the shrunken nucellus. Epidermal cells average about 70 by 20μ in surface view and 35μ radially.

Nucellus.—Elliptical in outline, borne on a short thick stalk about 0.45 mm. in diameter and 1 mm. long; apical end unknown; consists of a peripheral remnant of nucellar parenchyma externally surrounded by an epidermis with a well-defined cuticle and traversed by a prominent vascular system. Cells of epidermis somewhat larger than those of inner epidermis of integument, and

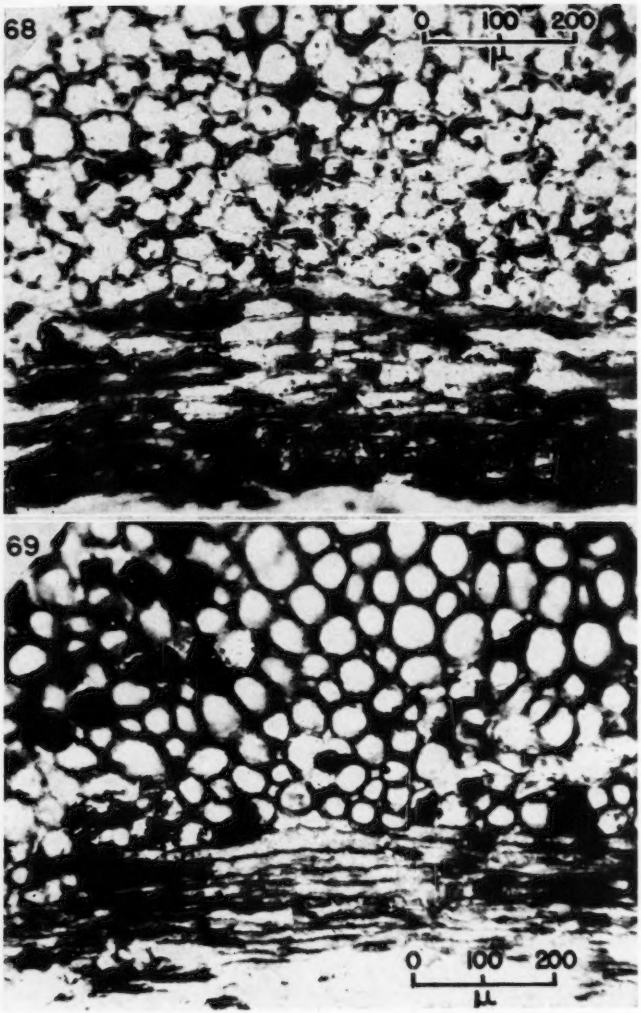


Fig. 68.—Tangential longitudinal section of *P. Noei* showing typical heavy parenchyma of the integument, above, and elongated fibrous cells of the inner stony layer, below. Near center of seed.

Fig. 69—From the same section as fig. 68 but taken near base of seed and shows, above, one of the numerous islands of stone cells which are present in the main fleshy layer. The stony layer, below, is similar to that in fig. 68.

its cuticle is somewhat thinner and lacks inward projecting intercellular cuticular deposits.

Vascular System.—A system of bundles supplies the integument and a second series supplies the nucellus. The nature of the basal vascular supply is unknown. The bundles of the integument are peripherally disposed, traversing the outer stony layer longitudinally to the tip; about 6-9 bundles in each of the 3 arcs of the integument between commissures (18-27 for entire seed). The position of bundles often is marked only by presence of lacunae of about 500μ in diameter with vascular elements destroyed. The chalazal bundle traverses the nucellus stalk and disperses in the chalazal disc to form a dense, radiating series of almost continuous vascular tissue. Bundles pass upward through the outer nucellar tissues at least three-fourths the length of the nucellus. Bundles composed of about 12-14 scalariform elements in radial section near the chalazal disc (fig. 71) and of about 6-8 elements nearer the top.

Spores and Pollen Grains.—Functional megaspore membrane, 18 to 20μ thick, lining the nucellar cavity. Non-functional megaspores and pollen grains unknown.

Locality and Horizon.—Upper Carboniferous, Allegheny Series, Harrisburg Coal, at Polk's Patch near Boonville, Warrick County, Indiana, Sunlight strip mine.

Material.—Two incomplete specimens found in coal balls sectioned in various planes by Reed (1939). A portion of Seed No. I, the best preserved of the 2 specimens, was kindly loaned to us for reexamination by Dr. Fredda D. Reed. Seeds and sections are in the collection of Dr. Reed.

Holotype.—Seed No. I.

Name of Species.—Pachytesta Noei, after the paleobotanist and collector, the late Dr. A. C. Noé.

This species, founded on the 2 specimens collected by Dr. A. C. Noé in southern Indiana near Boonville (printed by mistake as "Brownsville" in Reed, 1939, p. 777) is in overall appearance somewhat more slender than *P. vera. P. Noei* (Harrisburg, No. 5 coal) is slightly younger in age than *P. vera* from the Iowa coal ball horizon (Hoskins and Cross, 1943, fig. 40).

In Reed's account (1939) the specimens were referred to as Pachytesta No. I and No. 2. A picture of the external view of Pachytesta No. I appeared in Chamberlain (1935, fig. 23) under the name Trigonocarpus. This figure is reprinted here (fig. 67). It shows the base of the seed exposed in the fractured coal ball. A portion of the outer part of the integument (outer fleshy layer) is broken away exposing the external surface of the inner stony layer. The prominent pit represents the position of the chalazal bundle above the point of attachment. The ridge (rib) is the external expression of a radial extension of the stony layer.

A cut slice of this specimen showing on one side a near-median longitudinal surface through the seed was the portion made available to us for study. Reed's faithful pen portrayals of many of the minute details of organization through certain regions of this specimen (Reed, 1939, figs. 11-15) and those through portions of the less well-preserved Pachytesta No. 2 (figs. 16-23) must be referred to in any consideration of *P. Noei.*

We were fortunate in being able to identify the tissue represented at *il,*

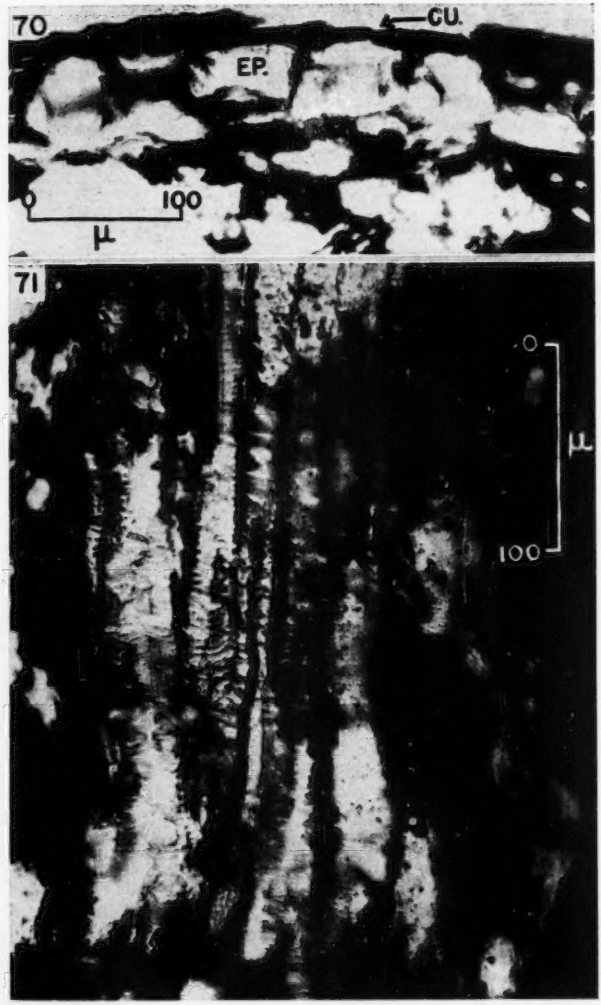


Fig. 70.—Portion of the cuticle (CU) and epidermis (EP) of the inner fleshy layer of the integument which has been partially destroyed before petrifaction. From upper part of seed. The inward projecting points of the cuticle are typical.

Fig. 71.—Longitudinal section of a vascular bundle of the nucellus taken just above the chalazal disc.

fig. 13 (Reed, 1939) as a portion of the inner stony layer, shown in greater extent in our figures 68 and 69, and in being able to demonstrate the strong vascular system of the nucellus (fig. 71). We have drawn heavily upon Reed's account for information concerning the number and position of the vascular bundles of the outer portion of the integument, to which our observations added but little. Some parts of the seed show a narrow peripheral zone of thinner walled cells external to (i.e., to the left of) the strong stony layer shown at *ol*, fig. 13 (Reed, 1939).

PACHYTESTA VERA Hoskins and Cross, Amer. Midl. Nat. 36(1):248-249, figs. 1-48, 51-53, 1946.

Organization.—Seeds large, radially symmetrical, ellipsoidal, 6.5 cm. long by 3.5 cm. in maximum diameter. Nucellus stalked and entirely free from the integument, occupying approximately three-quarters of the total length of the seed. Single vascular strand enters the base of the seed and branches to supply both integument and nucellus.

Integument.—Approximately 4.5 mm. thick throughout except in the micropylar area where it increases to 8 mm. Composed of a thick outer fleshy layer bounded by an epidermis with cuticle; a stony layer averaging 0.4-0.5 mm. thick except where radial extensions form three major longitudinal ribs extending from base to apex of seed, with occasional and irregularly placed secondary ribs; and a thin inner fleshy layer, except in micropylar area where it thickens greatly about the short micropylar tube. The inner fleshy layer is bounded by an epidermis with strongly developed cuticle.

Nucellus.—Bounded by an epidermis with cuticle; broadly dome-shaped at distal end, terminating in a short, centrally placed "beak" which projects into the base of the short micropylar tube. A definite opening, surrounded by special cells, provides a passage through the nucellar tissue to the unspecialized pollen chamber.

Vascular System.—Vascular bundles of the integument indefinite in number, varying from 18-36, etxending from base to apex, arranged in a single series near the periphery of the integument; adjacent to each major rib bundles may be more deeply placed. Nucellar bundles arranged in a single series near the periphery of the nucellus, radially flattened and extended tangentially, crowded or even overlapping in basal area. Bundles extend to base of pollen chamber. Vascular tissue of both series composed of scalariform or occasionally reticulated tracheids; bundles probably mesarch.

Spores and Pollen Grains.—Single, large, functional megaspore essentially filling nucellus; non-functional megaspores, arranged tetrahedrally, in nucellus above functional megaspore membrane. Pollen of the Florinites-type, averaging 63 by 45μ in equatorial plane, occur in numbers within pollen chamber.

Locality and Horizon.—Upper Carboniferous, Des Moines Series, near Oskaloosa, Mahaska County, Iowa. Angus strip mine.

Material.—Two more or less complete specimens and a portion of a third in calcareous petrifaction No. 1807. Seeds sectioned to expose 19 surfaces from which about 400 peel-sections were prepared. Housed in Paleobotanical Collection, Department of Botany, University of Cincinnati.

Holotype.—Seed No. I, petrifaction (coal ball) No. 1807.

The organization and histology of this species have recently been given in considerable detail in Part I. Further consideration here is unnecessary.

Pachytesta shorensis (Salisbury) Hoskins and Cross, comb. nov.

1914 *Trigonocarpus Shorensis* Salisbury, Ann. Bot. **28**:39-62, pl. 4, figs. 1-10; pl. 5, figs. 11-13, 16-20.

Organization.—Seeds large, radially symmetrical, ellipsoidal, tapered above and below, about 4 cm. long by 2.5 cm. in diameter, circular in transverse section. The nucellus is entirely free from the integument, is attached at the base by a very short, broad stalk (cushion), and occupies nearly one-half the entire length of the seed. A single vascular strand enters the base and gives off several branches to form the integumentary and nucellar vascular systems.

Integument.—Approximately 5 mm. thick in central region, 3 mm. in the lower portion and nearly 9 mm. surrounding the micropyle; composed of 3 principal layers: 1) an outer fleshy layer about 4 mm. thick in the middle of the seed, reduced below and expanded above, consisting of a peripheral hypodermal zone about 300μ thick (of sclerized fibers in groups of 2-6 cells radially, which often fuse laterally to form broad tangential sclerotic bands with interstitial parenchyma usually lost) overlaid by a thin-walled epidermis, and the main zone of rounded or irregularly stellate cells with numerous intercellular spaces more pronounced toward the outside (which occasionally form vertical lacunae). Innermost cells of inner fleshy layer (sarcotesta) are smaller and are direct continuations of rows of sclerized cells of 2) the sclerotic layer (sclerotesta). This tissue, 14-15 cells wide, averaging about 500μ in thickness is principally fibrous, made up of an outer layer of 5-9 series of evenly arranged cells which appear to be terminations of the inner zone of sinuous, intertwined, vertically elongated, thick-walled cells. Three longitudinal commissured ribs extending radially from the inner zone of the stony layer traverse the seed from base to apex, and alternating with these are 3 sclerotic extensions forming non-commissured ribs extending upward 8 mm. from the base. The sclerotic layer is enlarged at the base of the seed in the form of an inverted cone about 3.5 mm. high. This extends upward as the short stalk of the nucellus, 0.5 mm. high by 1.5 mm. in diameter. Internal to the stony layer, at least in the micropylar regions is 3) an inner fleshy layer of thick-walled cells which are more or less parenchymatous near the stony layer and which do not have dense contents. These line the short micropylar canal for its length of about 8 mm. Numerous secretory elements are scattered through the outer fleshy and stony layer of the integument.

Nucellus.—An ovoid body, narrowed at the base to its point of attachment to the nucellus stalk, about 18 mm. high by 11 mm. wide (maximum). Nucellus tissue represented principally by a thin-walled parenchyma, 200μ wide, interspersed with secretory ducts, traversed by a system of vascular bundles and the whole surrounded by a well-defined epidermis of cells 50μ radially by 30μ tangentially. This epidermis is often folded corresponding to the underlying files of secretory cells. A cuticle with short inward projecting points is often pulled loose from the epidermis.

Vascular System.—The main vascular strand, about 180μ in diameter, is composed of 60-70 elements, with larger tracheids at the periphery, and appears to be orientated with three points, possibly containing protoxylem, opposite the main ribs. The xylem is surrounded by 3-5 layers of elongated parenchyma cells. Six mesarch bundles of about 70 scalariform or reticulated elements are distributed (2 in each arc of the integument) midway between major and minor ribs near the limiting layer of sclerotic plates at the periphery. The main strand disperses radially at the base of the nucellus forming a tracheal sheath in the chalazal disc which soon becomes resolved into 12(?) discrete, mesarch bundles (4-5 scalariform and reticulated elements wide radially, and more tangentially) which pass upward nearly to the pollen chamber.

Spores and Pollen Grains.—Neither megaspores nor pollen grains recorded.

Locality and Horizon.—Lower Coal Measures, Short Littleborough.

Material.—Several petrified specimens from coal nodules.

Lectotypes.—Specimens figured by Salisbury (1914), pl. 4, figs. 1-10; pl. 5, figs. 11-13, 16-20.

Salisbury's excellent and detailed account presents most of the information necessary for an understanding of this species. The arrangement and structure of the sclerotized zones of the hypodermis of the integument and the extremely peripheral disposition of the bundles in the outer fleshy layer form an interesting corollary with *P. incrassata, P. gigantea* and *P. Noei.* The evident similarity of the inverted cone of sclerotic tissue at the base of the nucellus to *P. vera* is remarkable. The explanation of the absence of the inner fleshy layer in the middle region of the seed is difficult when it is so strongly developed at the apex. A smooth inner face of the stony layer is a common condition in other species in which an inner fleshy layer is present, a fact which, in addition to the presence of a strong opposing cuticle on the epidermis of the nucellus, might lead one to expect at least a thin inner fleshy layer to line the inner surface of the integument.

The "floor" of the pollen chamber, as we have suggested earlier (Part I), doubtless represents a phase in the disorganization of the apical parenchyma of the nucellus which is recognizable along the walls at the shoulders of the pollen chamber, according to his own account. The nature of the dispersal of bundles from the main vascular strand, as it enters the seed, to form the integumentary system is yet to be discovered. The apparent absence of at least some vestige of the megaspore membrane is unusual for generally it is a remarkably strong, well-preserved structure. The abundance of secretory elements in various regions is somewhat comparable to the secretory system of *P. vera.*

Pachytesta olivaeformis (Williamson) Hoskins and Cross, comb. nov.

1855 *Trigonocarpon* sp., in Hooker and Binney, Phil. Trans. Roy. Soc. London **145**: 151-153, pl. 4, figs. 1-17.

1877 *Trigonocarpon olivaeforme* Lindley and Hutton, in Williamson, Phil. Trans. Roy. Soc. London B, **167**:248-254, pls. 13-14, figs. 94-115.

1907 *Trigonocarpus Parkinsoni* Brongniart, in Scott and Maslen, Ann. Bot. **21**:96-124, pl. 11, figs. 1-8; pl. 12, figs. 9-15; pl. 14, figs. 24-32.

Organization.—Seeds medium-size, 3-4 cm. long by 1.3-1.6 cm. in diameter (of stony layer), radially symmetrical, ovoid. Nucellus short-stalked and

entirely free from the integument, occupying one-half the total length of seed. A single vascular strand branches to form both an integumentary and nucellar system.

Integument.—Total thickness unknown because of lack of preservation of outer portions, but at least 4 mm. in thickest areas; apparently thinnest in central part of the seed, expanding some at base and even more at top; composed of three principal regions: 1) an outer fleshy layer (sarcotesta) 1-2 mm. thick in center of seed, thicker in sinuses between ridges (ribs) of sclerotesta; made up of typical thin-walled parenchyma and usually mostly destroyed; inner part compact and without intercellular spaces, outer portion lacunar; surrounded by a strong hypodermis of 1-2 rows of large, palisade-like, radially elongated cells filled with dark contents, and a thin epidermis of small cells with a continuous cuticle. The outer fleshy layer abuts abruptly on 2) the stony layer (sclerotesta) in the central region of the seed and more gradually below and above. This sclerotic tissue, about 1 mm. thick at base, increasing to about 1.5 mm. at mid-portion and up to 2 mm. at apex, is mainly distinguishable in two layers, the innermost being very dark, mainly of vertically elongated, content-filled small cells (4-6 rows of vertically elongated, thick-walled, fairly uniform cells on the inside, a middle group of cells extending peripherally, and an outside zone of sinuous, tortuous, intertwined cells), and an outer main zone of larger, radially elongated cells forming a lighter colored palisade-like layer of sclerenchyma around the thinner inner zone. The entire outer portion of the sclerotesta is notably ridged with three major, commissured, ribs and 9 non-commissured radial extensions of the sclerotic layer which form 3 secondary ribs per arc of the integument, all extending from base to apex. Occasionally the middle secondary rib of each group of 3 is much reduced and may die out apically. On the inner surface of the sclerotesta 3 longitudinal furrows or grooves accentuate the position of the 3 main ribs. Internal to this multiple and remarkable stony layer is 3) an inner fleshy layer of delicate parenchyma, more prominent below than in the central region, and most prominent above and probably persistent throughout the length of the seed. At the apex a long micropylar beak, enclosed by the stony layer except at the micropylar opening, is recorded. In the petrified specimens known, it is comparatively short (about one-third the length of the seed). The base of the seed tapers below and appears to be extended asymmetrically into the stalk which bore it.

Nucellus.—Oval in outline, borne on a broad cushion of sclerotic tissue (sessile?), about 1 cm. in diameter by 1.5 cm. long, surmounted by a definite pollen chamber about one-tenth the height of the nucellus, and a nucellus beak about 500μ high with maximum aperture of 300μ. Nucellus wall thin but of fairly uniform width (100μ) up to the base of the pollen chamber. Wall composed of conspicuous epidermis (of longitudinally elongated (80μ), densely filled cells), covered by a cuticle which is usually pulled away, a zone of radially flattened, verically elongated parenchyma cells, and an innermost zone of tracheids.

Vascular System.—A single main strand enters the stalk-like base of the seed and soon gives off from the 3 angles of the chalazal bundle (as seen in transverse section) 3 strands which immediately bifurcate to supply 2 bundles

to each of the 3 valves of the integument. These bundles are opposite, and about 300μ radially from, the secondary ribs adjacent to the primary ribs. Bundles may possibly occur opposite the central secondary ribs for a total of 6 or 9 bundles (probably 6) which extend to the base of the micropylar region (?). The chalazal strand continues through the sclerotic cone into the base of the nucellus where it disperses completely forming a nearly continuous mantle which is resolved into discrete, radially flattened mesarch bundles which extend nearly to the pollen chamber.

Spores and Pollen Grains.—Within the nucellus is a dark colored structureless membrane representing the wall of the functional megaspore. No pollen grains have been found.

Locality and Horizon.—The Lower Coal Measures of various localities (from available reports). Lectotypes from the Lower Coal of the Lancashire field.

Material.—Numerous petrifactions in coal balls.

Lectotypes.—The three specimens figured by Hooker and Binney, 1855, pl. 4, in figs. 1-5; 7 and 11; 8 and 12. Housed in the Binney Collection, Cambridge, and the Geological Department of the Natural History Museum.

The specimens selected as the lectotypes are a part of the material studied by Hooker and Binney and constitute the first seed material known with structure preserved. Some of these specimens were restudied by Scott and Maslen (1907) and refigured (figs. 13, 14, 15 and 32) to show critical structures. Numerous other collections have been assembled and studied by Williamson, Oliver, Scott, Salisbury and others.

An examination of the material from Harrisburg, Illinois, described by Krick (1932) as *Trigonocarpus Parkinsoni* shows that this specimen is certainly similar in many respects to the descriptions of the British material of *Pachytesta olivaeformis*. The difference in geological horizon, however, is considerable (see Hoskins and Cross, 1943, fig. 40), and there are certain anatomical differences. Unfortunately the sections prepared from Krick's specimen fail to exhibit all critical areas. Certainty as to identification should probably await further investigation.

The selection of the name *P. olivaeformis* follows the rules of botanical nomenclature. Williamson applied this specific epithet to the material which he described (1877) and which he stated was the same as that described earlier, without a specific name, by Hooker and Binney (1855). His basis for the selection of the specific name was the apparent superficial resemblance of his specimen to the seeds described by Lindley and Hutton (1837, 3: pl. 222, figs. 1, 3) from structureless casts. Such a comparison cannot logically be made. Later (1907) Scott and Maslen considered this and additional material and concluded on the basis of apparently adequate evidence that the name *T. olivaeforme* was a synonym of *T. Parkinsoni* Brongniart (1828). He consequently transferred the name *T. Parkinsoni* to Williamson's material, to that of Hooker and Binney and to his own (all considered to be the same species as determined from structure), a name also based on material known only as structureless casts and therefore not surely identifiable with structural material. In transferring all such seeds known from structure from the genus *Trigonocarpus* to the genus *Pachytesta* the first valid name used for this species of

fossil seeds known from structure, *olivaeforme*, is available. The specific name *Parkinsoni* becomes a synonym. The name *Trigonocarpus Parkinsoni* Brongniart is still retained for seeds of a certain type (described earlier in this paper) which are known only as casts, compressions or impressions and without adequate structure. The name *T. olivaeforme* is invalid as it was a synonym when established. *Pachytesta olivaeformis* cannot be compared specifically with any species of Trigonocarpus.

Of the seven genera at present included within the genus Pachytesta, *P. olivaeformis* stands somewhat apart in the 1) thickness and organization of the stony layer, 2) the number and persistence of the secondary ribs, 3) the deeply placed integumentary bundles, 4) the stalked nature of the seed (Scott and Maslen, 1907, pl. 12, fig. 12), and 5) the extended micropylar beak. The weight of these variations, however, when all characteristics are considered, appears insufficient to isolate this species from the generic group.

VI. Other Genera of the Trigonocarpales

This study of the Pachytesta-Trigonocarpus complex has demonstrated the necessity for classifying under distinct names those fossil seeds found with structure preserved and those which can be identified on the basis of external and/or superficial characteristics only. We have suggested above that a number of common types of fossils (casts, compressions, etc.) may be derived from a single seed based on its anatomy and course of fossilization, and, conversely, that a similar type of fossil may be derived from any one of several seeds. A reasonable method of approaching these problems has been suggested by our proposals concerning Pachytesta and Trigonocarpus. It is not the purpose of this paper to consider all of the genera which have been referred to the Trigonocarpales. We will, however, briefly review a number of genera and suggest their principal generic delimitations.

We recognize the probability that later studies of seeds with structure preserved will show that the group presently included within the Trigonocarpales is an unnatural plant assemblage with forms which may be unrelated. It is also probable that the examination of additional material may result in the consolidation of one or more genera into a single genus. At the present, however, we shall consider 9 genera which have been recorded as members of the Trigonocarpales based on common structural characteristics as given on p. 336, paragraph 4. We also suggest for consideration 5 groups (genera?) to include some of the commoner, more identifiable, variously preserved remnants of seeds known from casts, compressions or impressions, for which many generic names have been proposed by Seward, Arber and many others.

The genera shown in figures 57-65 have in common those characters previously reviewed (p. 336, par. 4). These figures are of the same size to facilitate their comparison. The scale given for each is approximate for an average species when more than one is known. The presence and extent of certain tissues have been conjectured (indicated by dotted lines) for several incompletely known genera. The nature of the outer fleshy layer is unknown in some of these, and in others it is based on information derived from fragmentary vestiges remaining on those parts of the seeds not generally well

preserved, e.g., in the perimicropylar groove in Stephanospermum and in the sinuses between the ribs in Codonospermum. In many instances the loss of the integumentary vascular system accompanies the disappearance of this layer. Frequently the study of a considerable number of specimens has been necessary to prove the presence of bundles in the integument.

Generic differences between such forms as Hexapterospermum and Polypterospermum are not clear. The nature and number of the commissures and principal ribs, the basic distinction at present, will require study of additional material. It is interesting to note that all but one of these genera, Rotodontiospermum Arnold and Steidtmann (1937), were founded by Brongniart (1874a) for petrified seeds from the silicified magmas of St. Étienne and some of the descriptions were based on single specimens. Subsequent study and descriptions by Renault, Williamson, Kidston, Oliver, Scott, Maslen, Bertrand, Arber, Salisbury and others have made the nature of some of these more certain.

The drawings in figs. 57-65 are arranged arbitrarily according to the nature of the commissured ribs. Stephanospermum and Aetheotesta have an uninterrupted ring of sclerotic tissue within the fleshy layer. The integuments in these, therefore, lack commissures. These two have additional characteristics which aid in their generic identification. In Stephanospermum the conspicuous perimicropylar collar of the stony layer is well known (more prominent in Brongniart's species, *S. achenoides* than in *S. caryoides* Oliver), and the presence of a tracheidal mantle completely investing the nucellus is recorded (rather than discrete bundles above the chalazal disc). The development of the lacunar zones in both micropylar and chalazal areas in Aetheotesta is greater than in other allied seeds. The only comparable condition is found in the genus Sarcospermum (Deevers, 1937) which appears from a preliminary examination to be practically indistinguishable from Aetheotesta.

Pachytesta as shown in figure 59a is a composition including some of the several variations characteristic of different species. The arc of the integument showing no secondary ribs and numerous vascular bundles (upper right) represents the condition obtaining in *P. incrassata*, *P. gigantea* and *P. Noei;* the lower arc representing *P. olivaeformis* shows three prominent ribs in the midsection and deeply placed integumentary bundles; the organization of these tissues in *P. shorensis* is diagrammed in the arc at upper left. Figure 59b is in general representative of the entire genus but is based primarily on *P. vera.*

Hexapterospermum, Polypterospermum, Ptychotesta and Polylophospermum are all similar in having primary ribs in multiples of three. It is usually possible to distinguish primary ribs from secondary ribs by the presence of a commissure or lacunar zone extending radially (and more or less longitudinally elongated) through the integument. Some sections across a seed may fail to show these, and they may be difficult to determine in the case of an immature seed. However, mere radial extensions of the stony layer are of much less importance than is the presence of a commissured rib, for such extensions vary greatly even in the same species. In the earliest report on Hexapterospermum none of the 6 ribs was reported to have commissures, a condition used as one of the bases for generic separation from Ptychotesta. Later study of the same material and an examination of one of Brongniart's own figures

show the occurrence of sutures in some of the ribs. The importance of the peltate ribs as seen in transverse section (62a) of Ptychotesta is probably questionable. The material used as the basis of description was very poorly preserved. The slightly hexagonal outline of Polypterospermum indicates that commissured ribs rather than flanges might be sought at the angles. If this should be the case, then it is quite similar to Hexapterospermum, the minor ribs being of secondary importance. If no commissures do exist then it probably should follow the non-commissured forms, Stephanospermum and Aetheotesta in the series shown.

Only in external form is Polylophospermum markedly different from the other seeds with six major ribs. This genus has been studied in considerable detail. Many of its histological features are quite similar to those of Pachytesta, and in transverse section it resembles Hexapterospermum. However, the unusual development of the entire integument at the apical end to form a micropylar chamber is distinctive. Basal extensions of the stony layer, appearing as "heels" in figure 63b, are reported to be part of a peribasal flange, although they may be parts of the main ribs as seen in an obliquely tangential section.

Codonospermum, figure 64, is an 8-angled seed within the basal portion of which is a large air chamber. The transverse section represents a level through the mid-portion of the nucellus. No fissures in the ribs are reported, and the full extent of the outer flesh is unknown. The main body of the seed is more globose and the micropyle is relatively shorter than in most of the genera of the Trigonocarpales. It is possible that this genus should not be referred to this group. Another 8-ribbed seed, Eriotesta, is not figured here because of its doubtful nature.

Rotodontiospermum, found in the McLeansboro Formation of Illinois, has an unusually large number of ribs which traverse the seed longitudinally. An examination of this material gives no reason to believe that it was commissured, and the inner outline of the stony layer is circular in transverse section as in Aetheotesta and Stephanospermum. The large number of deeply placed bundles alternating with the sclerotic ridges is a most distinctive feature. The histology of the various tissues is comparable to corresponding tissues in some species of Pachytesta. The peripheral region of the seed, a radial continuation of the inter-ridge parenchyma, is poorly preserved in most specimens.

The possible fossil forms which may result from different modes of preservation of seeds illustrated in figures 57-65 are many. Casts of the inner surface of various tissues differ greatly from molds or casts of their exterior surfaces. Internal casts of the integument of Aetheotesta, Codonospermum, Rotodontiospermum and Stephanospermum would be smooth, those of Pachytesta, 3-ridged, etc. External casts of the stony layer of Rotodontiospermum and perhaps Polypterospermum would appear many-ribbed, whereas Pachytesta might be 3-ribbed (*P. vera*) or 12-ribbed (*P. olivaeformis*), especially if the commissured primary ribs were somewhat deteriorated, a common condition. One cast of a very large seed from Ohio, *Trigonocarpus steecensis* W. Berry (1932) shows 3 "double ribs" and 3 secondary ribs which might be derived from unequally commissured ribs of Hexapterospermum or from a cast of the external surface of the stony layer of Pachytesta. A species of Hexapterosper-

mum recorded by Arnold (1937) from the Sharon Coal of Ohio showed 6 ridges on the carbonized remains of the testa. As 3 of these ridges were more prominent this specimen might well have been derived from a Pachytsta. It is a form which would fit within the generic limits of Trigonocarpus as we have defined it.

External casts or compressions of any of these seeds except Polylophospermum and Stephanospermum might show an essentially smooth surface with nerve-like striations on the surface as shown in figure 49. This is of the Neuropterocarpus-type which has been discussed in connection with Pachytesta (p. 331, par. 3). A multi-ribbed seed of the Holcospermum-type (fig. 55) could be derived from an external cast of the stony layer of Rotodontiospermum or possibly Polypterospermum or from an internal cast of the nucellus of any of several of the genera where the strong nucellar vascular tissue is effective.

Finally, then, these five, the Neuropterocarpus-type (fig. 49), the Holcospermum-type (fig. 55), the Carpolithus-type (fig. 56), the Trigonocarpus-type (figs. 50-54), and the Polypterocarpus-type (of Grand 'Eury, 1877, pl. 15, fig. 8, showing 6 or more deep flanges) are the fossil forms most commonly found which can be derived through the vicissitudes of preservation from those genera of the Trigonocarpales known from structure.

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The Role of Wood Anatomy in Phylogeny

Oswald Tippo

During the past three decades, plant anatomists have established a number of lines of phylogenetic specialization in the structures of the stele. Just as the taxonomists have worked out certain trends in the evolution of the flower—for example, the change from spiral to the cyclic arrangement of the floral organs, from free floral parts to fused floral organs, from hypogyny to epigyny, etc.—so morphologists have described the following lines of anatomical specialization:

1. The prostostele is more primitive than the siphonostele or the dictyostele (i.e., eustele of Brebner) (Jeffrey, 1897, 1917).

2. In the Angiosperms, the woody stem of trees and shrubs is more primitive than that of herbaceous plants (Eames, 1911; Sinnott and Bailey, 1914, 1922; Jeffrey and Torrey, 1921, 1921a).

3. The vessel element with scalariform perforation plates appeared in plants before the vessel member with a single opening in the perforation plates (Jeffrey, 1917; Bailey and Tupper, 1918; Frost, 1930, 1930a).

4. Among the vessel elements with scalariform perforation plates, the type with numerous bars and narrow openings is more primitive than the type in which there are few bars separating wide openings or perforations (Frost, 1930a).

5. The vessel elements which are long, small in diameter, and angular in cross-section preceded those which are short, broad, and circular in cross-sectional outline (Bailey and Tupper, 1918; Bailey, 1920; Frost, 1930).

6. Vessel elements with long, sloping end-walls are more primitive than those with end-walls which are transverse (Bailey and Tupper, 1918; Frost, 1930, 1930a).

7. The phylogenetic order of the several types of pitting on the side walls of the vessels is scalariform, transitional, opposite, and finally alternate (Bailey and Tupper, 1918; Frost, 1930, 1931).

8. The type of vessel arrangement in which the pores occur singly throughout the wood (i.e., solitary pores) is less advanced than the various aggregate groupings, such as pore multiples, pore clusters, and pore chains (Frost, unpublished data).

9. The diffuse-porous condition is more primitive than the ring-porous state (Frost, 1930; Gilbert, 1940).

10. Evolution has proceeded from tracheids to fiber-tracheids to libriform wood fibers (Jeffrey, 1917; Bailey and Tupper, 1918; Bailey, 1936). Accompanying this development there has been a progressive decrease in the length of these elements (Bailey and Tupper, 1918; Bailey, 1920).

11. So far as the several categories of tracheids are concerned, the phylogenetic development in the Angiosperms has been from scalariform tracheids to circular bordered pitted tracheids (Jeffrey, 1917).

12. The diffuse arrangement of wood parenchyma cells is more primitive than are the various aggregate arrangements, such as banded apotracheal and

the various paratracheal types, such as vasicentric, aliform, and confluent, (Kribs, 1937).

13. Heterogeneous rays, that is, rays with vertically elongated cells as well as radially elongated cells, are less specialized than are homogeneous rays, that is, rays in which all the cells are radilly elongated (Kribs, 1935; Bargheoorn, 1940, 1941, 1941a). Kribs (1935) has shown that the evolutionary sequence is from heterogeneous type I, the most primitive, through the transitional heterogeneous types IIA and IIB, to homogeneous type I, and thence to the highly specialized homogeneous type II rays.

14. Woods with non-stratified cells are more primitive than those with storied structure (Bailey, 1923).

Before proceeding to a consideration of the utility of these phylogenetic sequences, it will serve a useful purpose at this point to discuss briefly the methods by which these salient lines of structural specialization have been established. Several of these trends have received support from paleobotany. Thus, we know from the study of fossils that plants with protosteles appeared on the scene before those with siphonosteles, or those with dictyosteles. Looking back to the Devonian and Silurian we find that such genera as Rhynia, Hornea, and Asteroxylon of the Psilophytales—the most primitive vascular plants of which we have any record—possess protosteles. Sinnott and Bailey (1914) have shown that in the Angiosperms the primitive arboreal forms gradually lost their cambial activity with the result that herbaceous plants developed in this group. The fossil record, also, supports the trend involving the types of tracheids, for scalariform tracheids are common in fossil fern material, while tracheids with circular bordered pits attain their best development in the Gymnosperms. Furthermore, a survey of extinct plants shows that tracheids were the first and only constituents of wood, that fiber-tracheids appear for the first time in the Gymnosperms, and that libriform wood fibers are not encountered until we reach the Angiosperms. It appears, therefore, that the trends involving the types of stele, the origin of the herbaceous habit, the types of tracheids, and the evolution of fibrous elements have a good paleobotanical basis.

Many of these phylogenetic sequences receive support from the field of comparative morphology. Thus, protosteles are found in greater abundance in such groups as the club-mosses and the ferns—groups which are considered to be primitive vascular plants on the basis of all the evidence. Sinnott and Bailey (1914) have compiled a massive array of comparative data which indicate that herbaceous stems were derived from woody ancestors. A study of living forms also demonstrates that scalariform tracheids are less specialized than the type with circular bordered pits, and that tracheids are the only fibrous elements in steles until we reach the Gymnosperms, and that libriform wood fibers appear for the first time in the Angiosperms.

In the past, developmental data have often been cited as evidence for the validity of these lines of structural modification. Thus, in many plants where the mature stele is a siphonostele, a protostele precedes it in ontogeny. Other plants with dictyosteles in their adult condition begin as protosteles. It is a well known fact that in the development of the primary xylem of Angiosperms, the first wood cells to differentiate are elements with rings or spirals,

followed by scalariform tracheids, and finally the last formed elements bear circular bordered pits on their lateral walls. Again, in a given growth ring of oak wood, for example, the first formed wood, or early wood, contains tracheids, which are then gradually replaced by fiber-tracheids, and these in turn give way to libriform wood fibers. In a similar fashion, woods which are characterized by vessel elements with simple perforation plates, often have a few scalariform plates in some of the early growth rings, or in the primary xylem; while woods which have homogeneous rays in their mature regions, may have heterogeneous rays in their earlier areas (Barghoorn, 1940).

While several of these trends were established on the evidence from the fields of paleobotany, comparative morphology, and developmental anatomy, most of these sequences were built up by another method. This latter method finds its origin in the work of Bailey and Tupper (1918), an extensive study of cell size in hundreds of plants occurring in all the major groups of the Tracheopnyta, or vascular plants. This very thorough and most fundamental study revealed that the length of tracheary elements—that is, tracheids, fibers, vessel elements, etc.—decreases as one proceeds from the lower to the higher vascular plants. In other words, it was disclosed that the wood cells of the so-called vascular cryptogams are very long, those of the Gymnosperms more or less intermediate in length, while those of the Angiosperms are relatively short. Furthermore, the evolutionary specialization of the vessel element proceeds hand in hand with this reduction in length of the tracheary cells, that is, as the tracheary elements decrease in size, the vessel members pass from the scalariform to the simple perforate state, they bcome wider, the pitting on their lateral walls changes from scalariform to transitional to opposite to alternate, and their end-walls become less and less tapering. This earlier work pointed out—and Bailey (1944a) has just recently emphasized the fact anew—that the appearance and subsequent evolution of the vessel element is strikingly correlated with the decrease in cell size. For example, in those highly interesting vessel-less Angiosperms, Trochodendron and Drimys, the tracheary elements are longer than those of any other Dicotyledon studied. On the other hand, the Gymnosperms which possess vessels, namely the Gnetales, have fibrous elements which, in length, resemble those of many Dicotyledons. Finally, Bailey and Tupper indicated that correlated with this decrease in size of wood cells and with this evolution of the vessel, there is a progressive specialization of the fibrous tracheary elements, that is, the bordered pits become smaller and smaller, until ultimately a libriform wood fiber with simple pits is produced.

Using the research of Bailey and Tupper as a basis, Frost (1930, 1930a, 1931) has shown that the specialization of the other features of the vessel elements is synchronized with the progressive shortening of the tracheary cells. Later, Kribs (1935) demonstrated that the trend from heterogeneity in rays to homogeneity was paralleled with decrease in cell size, as well as with the specialization of the vessel members, and of the other tracheary elements. Still later, Kribs (1937) showed that the sequence from the diffuse parenchyma arrangement to the apotracheal and paratracheal types is also synchronized with the evolutionary development of vessels.

The point that I wish to make—and Turrill (1942) has recently under-

lined its significance—is that the direction of these lines of specialization has been established either by grounding them on paleobotanical, comparative morphological, and developmental studies of all the vascular plant groups, or else they have been established by correlating them with the progressive decrease in cell size which has been demonstrated for the Tracheophyta. In other words, these evolutionary trends are not based on any system of Angiosperm classification, but have been formulated independently of any preconceived notion that this or that group of Gymnosperms has given rise to the Angiosperms; or any preconceived idea that the Ranales or the "Amentiferae" are primitive. Consequently, any suggestions which the anatomist makes will be relatively free of bias, and therefore of correspondingly greater value than would be the case were not his methods founded independently of Angiosperm classification.

At this point we logically arrive at a consideration of the manner in which these lines may be used in phylogenetic studies. In actual practice, the method employed may be described in the following terms: The anatomy of a given group is investigated, particular attention being given to those characters involved in the sequences already described, although other characters may prove to be useful, too (Tippo, 1941). Next, the pertinent phylogenetical schemes of the systematists, usually based on floral morphology, are examined. Then, data are accumulated from other branches of botany, such as paleobotany, cytology, nodal anatomy, pollen morphology, embryology, developmental anatomy, etc. The relationships of the several taxonomic entities under consideration are then interpreted in the light of the trends of structural specialization, and an attempt is made to harmonize the evidence derived from the various fields. In other words, instead of basing phylogenetical conclusions on the structure of one part or organ, the evidence secured from all parts of the plant is employed.

It cannot be too strongly asserted that the use of this method is not an attempt to substitute anatomical characters for those of external morphology. The anatomist admits readily that if he were rash enough to attempt the creation of a phylogenetic system based on features of the vascular system alone, some very weird results would crown his efforts, at least weird as viewed from the standpoint of our present concepts of classification. This is attributable to the fact that vessels and other wood structures have undoubtedly undergone similar phylogenetic development in unrelated groups. In other words, parallel and convergent evolution have occurred. Consequently, the presence of simple perforation plates in the vessels of two groups does not necessarily imply genetical affinity. Of course, similar situations obtain in classifications founded on flower structure. It has, therefore, become increasingly evident that claims that flowers, or vascular structures, or that some parts of plants are universally more conservative than other parts are unrealistic. Rather it appears, as Bailey and Howard (1941c) have pointed out, that the rates of phylogenetic change differ in the various parts and organs of plants, and thus the development of one structure may be accelerated or retarded in comparison with the evolution of other regions in the same plant or group of plants. Furthermore, there is no constant relationship among these rates, for in some groups the flower forges ahead, while the wood lags; whereas in other

groups, the anatomical features may develop at a more rapid rate. Consequently, in our endeavors to construct a natural system of classification we must consider, and weigh carefully, and harmonize, and integrate the evidence from all parts of the plant, and from all branches of botany, including anatomy, genetics, cytology, physiology, embryology, paleobotany, etc.

At this juncture we may with profit turn to a consideration of a few specific cases where the utility of these anatomical lines has been demonstrated in phylogenetic studies. We may very well begin with the problem of the origin of the Angiosperms, or the "abominable mystery" as Charles Darwin styled it. Are the Magnoliales primitive as asserted by Hallier, Bessey, and Hutchinson; or are the "Amentiferae" the least specialized, as indicated by Engler and Prantl, and by Wettstein? The bulk of the evidence from the study of wood anatomy supports the former hypothesis, for by and large the Magnoliales have a very primitive array of anatomical characters. Some of the genera lack vessels, while most have scalariform perforation plates exclusively. The vessel elements are characterized by great length, small diameter, steep end-walls, angular cross-sectional appearance, and scalariform intervascular pitting. The woods are diffuse-porous, and the pores have a predominantly solitary arrangement. The fibrous tracheary elements in many species are tracheids exclusively; all such elements are very long. Many of the plants in this group have heterogeneous rays. Some of the species have diffuse parenchyma. Almost all forms are arboreal in habit. On the basis of wood anatomy, therefore, there is much to recommend the Magnoliales as a very primitive order among the Dicotyledons. On the other hand, many of the members of the "Amentiferae" have porous perforation plates exclusively on their vessel elements, they are ring-porous, and their vessel members are often short, round, large, and with opposite or alternate pitting. Fiber-tracheids and libriform wood fibers prevail, as do homogeneous rays. In other words, the "Amentiferae" are rather highly specialized from the standpoint of wood anatomy (Tippo, 1938). Then, when it is recalled that Eames (1929) and his students (Fisher, 1928, 1928a; Bechtel, 1921; Abbe, 1935; Manning, 1938, 1940; Boothroyd, 1930) have published a series of papers on the floral anatomy of the "Amentiferae" which indicate that the members of the Salicaceae, Urticales, Betulaceae, Juglandaceae, and Platanaceae possess highly specialized flowers, having undergone extreme reduction through the loss of sepals, petals, stamens, carpels, ovules, etc., we can say that as far as anatomy is concerned there is little to recommend the "Amentiferae" as a primitive group of Angiosperms. On the contrary, the available evidence (Tippo, 1938) indicates that some of the "Amentiferae," at least the Casuarinales, Fagales, and Urticales, are derivatives of the Hamamelidaceae, which, in turn, are derivatives of the Magnoliales.

Wood anatomy has assisted in the phylogenetical placement of other groups. For example, the Rhoipteleaceae have been placed in the Urticales by some students of the family, and in the Juglandales by others. Withner (1941) investigated the anatomy of the family, and on the basis of this study concluded that they belong to the Juglandales for the Rhoipteleaceae have scalariform perforation plates, which are also present in the Juglandales but are lacking in the Urticales. The aromatic glands and the pinnately compound leaves of the

Rhoipteleaceae constitute further evidence that this family belongs with the Juglandales.

The Eucommiaceae have been placed traditionally in the Hamamelidales, although some systematists have suggested that the family should be classified with the Urticales. The anatomy of these groups has been investigated (Tippo, 1940), and the conclusion has been reached that the family should be assigned to the Urticales. The Eucommiaceae have vessel elements with simple perforation plates, and latex; characters found in the Urticales, but absent from the Hamamelidales.

Vestal (1937, 1940) investigated the families assembled by Engler in the Parietales, and found that Wettsteins' division of this heterogeneous order into the Parietales and the Guttiferales is sound on the basis of the anatomical evidence.

Employing the methods already outlined, Heimsch (1942), in an extensive study of the comparative anatomy of the wood of the Gruinales and the Terebinthales, concluded that the Burseraceae, Meliaceae, Sapindaceae, Rutaceae, Simarubaceae, and Anacardiaceae constitute, on the basis of their wood structure, a phyletic unit. Therefore, the classification of Engler which places some of these families in the Geraniales and others in the Sapindales is not supported. Support, however, is given to Wettstein who places the families in the Terebinthales, and to Hutchinson, who puts them in the Pinnatae. Heimsch concluded further that the Julianiaceae are close to the Anacardiaceae, but that the Juglandaceae are not closely related to either of these two groups. He also suggested that the Simarubaceae may not be a natural family since there is extreme diversity in the xylem.

The examples cited thus far have been connected with extensive exploratory investigations of orders, or of larger complexes, in which the phylogenetic unit was the family. In other words, the pawns which were moved here or there in the phylogenetic chess-game were families and orders, and no attempt was made to go below the family level. However, there have been a few intensive studies in which this same method has been used within specific families with promising results, provided the families selected possessed a significant range of structural variability. For example, Heimsch and Wetmore (1939) have investigated the Juglandaceae and have shown that while certain anatomical characters are more or less constant throughout the family, significant differences do exist among the genera. As a matter of fact, the anatomical data were in striking accord with the conclusions of Manning (1938) based on the organization of the inflorescences.

Heimsch (1940) has also studied the genus Rhus and its allies, and again has found that these genera have certain common structural features, but that there are salient differences among the genera. His study of the xylem, and the pollen of the Rhus complex supports Barkley's taxonomic conclusions, and serves to emphasize again, the fact that supplementary morphological investigations may furnish the taxonomist with valuable data.

Undoubtedly, the best illustration of the efficacy of the anatomical method with its associated harmonization of the evidences from floral morphology, cytology, paleobotany, and other related fields is offered by the cooperative investigations of Bailey, Howard, Smith, and Nast (Howard, 1940; Bailey

and Howard, 1941, 1941a, 1941b, 1941c; Bailey and Nast, 1943, 1943a, 1944, 1944a, 1945, 1945a; Bailey, 1944; Nast, 1944; Nast and Bailey, 1945; Bailey, Nast and Smith, 1943; Bailey and Smith, 1942; Smith, 1945). In their numerous papers on the Degeneriaceae, Himantandraceae, Winteraceae, and Trochodendron and Tetracentron, the following conclusions have been reached: The newly described genus Degeneria belongs to a separate family, the Degeneriaceae, which is closely related to the Magnoliaceae. The Degeneriaceae, Himantandraceae, and Magnoliaceae (sensu stricto) are closely related, while the Winteraceae show only remote relationship to the Magnoliaceae, and therefore the various genera of the Winteraceae should not be placed in the Magnoliaceae as has been done in the past. Trochodendron and Tetracentron are very similar structurally, but these two genera are quite different from the Winteraceae and should be removed from that family. Illicium, which has vessels, should be divorced from the vessel-less Winteraceae and should be classified in a different family. Euptelea exhibits no significant similarities to Tetracentron and Trochodendron and therefore should not be associated with these genera. The latter two genera are not closely related to the Magnoliaceae (sensu stricto), Degeneriaceae, Himantantraceae, Winteraceae, Schisandraceae, Cercidiphyllaceae, or Eucommiaceae.

Bailey (1944a), who has been the leader in this field for three decades, is of the opinion that these lines of structural modification are now so reliably established that they are to be reckoned with in considering any phylogenetic theories pertaining to the Angiosperms. He states that "the fact that structurally primitive angiosperms had scalariformly pitted tracheids, from which vessels originated, rules out any possibility of deriving the angiosperms from the Gnetales or other known representatives of the higher gymnosperms. The Ginkgoales, Coniferales, and Gnetales are characterized by having a highly specialized and peculiar type of primary xylem which is entirely unlike that of other known vascular plants with the possible exception of the Ophioglossales." In this connection, it is significant that Andrews (1940)—impressed with the weight of these lines of structural modification—in his work on the Pteridosperms, refrained from speculating on the phylogenetic connection between this group and the Dicotyledons, because the former lack scalariform tracheids in the secondary wood.

Bailey continues as follows: "The independent origins and specializations of vessels in monocotyledons and dicotyledons clearly indicate that, if the angiosperms are monophyletic, the monocotyledons must have diverged from the dicotyledons before the acquisition of vessels by their common ancestors. This renders untenable all suggestions for deriving monocotyledons from vessel-bearing dicotyledons or *vice versa*. Furthermore, the highly specialized structure of the xylem throughout both stems and roots of herbaceous dicotyledons, not only affords conclusive supplementary evidence of the derivation of herbaceous from arboreal or fruticose dicotyledons, but also is an insuperable barrier to the derivation of monocotyledons from herbaceous dicotyledons.

"Similarly, the occurrence of primitive vascular structures in a given genus, family or order renders untenable suggestions for deriving such plants directly from structurally more highly specialized ones."

Dadswell (1939) and Record (1934, 1935) have both cited numerous

additional examples of the contributions which the study of anatomy has made to classification. But perhaps enough has been said to reveal that in the groups investigated considerable light has been thrown on the phylogenetic problems involved. It is to be hoped that the work will continue until all the woody groups of the Dicotyledons have been re-examined in the light of these salient lines of anatomical evolution. It is also hoped that similar series will be worked out for other parts of the vegetative body, such as the phloem—where some progress has been made with the types of sieve-tube cells—the root, the leaf, the primary body, and other parts. Indeed, further improvement and refinement of our knowledge of some of the sequences of specialization in the secondary xylem itself would be helpful in future investigations. For example, whereas we know that the diffuse arrangement of wood parenchyma is more primitive than the various aggregate configurations, we are in ignorance with respect to the exact phylogenetic relationships among the apotracheal and paratracheal types. The same situation prevails in the case of the several types of vessel distribution.

The next logical development which may be expected in this field of endeavor is a series of extensive exploratory investigations of the herbaceous Dicotyledons whose purpose will be not only to uncover new phylogenetic sequences, but to extend the lines of specialization already established into this relatively virgin territory. There is every reason to suppose that the trends already defined will be found to prevail in the secondary wood of the herbs, and there is also some basis for the belief that similar sequences will be unearthed in the primary xylem. Bailey (1944a), for example, has recently shown that the evolutionary development of the vessel elements in the primary xylem parallels the development of these structures in the secondary xylem.

So far as the Monocotyledons are concerned, a very significant beginning has already been made by Cheadle (1942, 1942a, 1943, 1943a, 1944; Cheadle and Whitford, 1941). He has shown that the salient lines of evolution which have been defined for the secondary body of Dicotyledons also play their part in the primary xylem of the Monocotyledons, and he has detected a few additional lines, such as those involving the nature of secondary growth and the form of the vascular bundles. Little more preliminary work will be required before he and others will be able to tackle the many unsettled phylogenetic puzzles in the Monocotyledoneae.

The development of these anatomical concepts should give a new impetus to the study of fossil Angiosperm woods. The identification and the systematic assignment of fossil woods rests, of course, upon a knowledge of the woods of living Dicotyledons, and, therefore, these salient trends of structural modification should be of great service in the study and interpretation of fossil woods. Already Edwards (1931) has made a good beginning by compiling a list of all the described fossil dicotyledonous woods. But as Hamshaw Thomas (1936), Miss Bancroft (1932), and Bailey (1924) have emphasized, the majority of these fossil woods were studied and named at a time when our knowledge of wood anatomy was far from complete, and consequently their suggested affinities are very dubious indeed. Therefore, material already described, and previously untouched fossil woods should be examined in the light of the developed lines of specialization. These trends should prove to be

of great aid in interpreting this material, and in assigning the different woods to their proper systematic position, for while it is true that many structural features occur in unrelated groups, it has not been demonstrated that identical combinations of anatomical characters occur in such groups (Bailey, 1924). Andrews (1940), although investigating the Pteridosperms, found that these lines of evolutionary development were of considerable assistance in the study and interpretation of the anatomy of this order of seed plants.

It is to be expected that similar paleobotanical investigations will not only be facilitated by the lines already defined, but that these investigations in turn will contribute to our knowledge and understanding of the established lines of specialization. Chalk (1937) , for example, has made a survey of all described dicotyledonous fossil woods, and has shown that the proportion of woods with scalariform perforation plates is higher among the recorded fossil Dicotyledons than among modern genera. It is gratifying to learn that a character considered to be primitive by the wood anatomist on the basis of other evidence was relatively more common in past geological time.

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Taxonomy of Tertiary Flowers and Herbaceous Seeds

Maxim K. Elias

The classification of fossil flowers and seeds is greatly handicapped, if not made entirely impossible, when their remains are found in a flattened, crushed state of preservation. Unfortunately, this is almost invariably the case with fossil flowers, and is frequently also the case with fossil seeds. In flattened flowers the delicate stamens and pistils usually overlap and appear crushed and the taxonomically important details are thus not preserved.

The conclusion of a paleobotanist, when identifying such remains, reads usually like this: "Flowers, affinities unknown." Only a few of the numerous fossil flowers from the late Tertiary of Europe and adjacent isles, described mostly by Heer, are referable to herbs. His cautious taxonomic attitude, as exemplified by such names as *Borraginites myosotiflorus* (Heer, 1855-1859), implies only broad affinity to living Boraginaceae, — and is the best possible treatment for such remains. The difficulties involved in the identification of fossil flowers are fully discussed by Cockerell (1911-1913) in the light of examples from the Tertiary Florissant Lake deposits of Colorado.

In 1935 (p. 122) Hamshaw Thomas pointed out that paleobotanical evidence failed to disclose any flowers with micro- and megaphylls arranged spirally on an elongated axis, a hypothetical floral structure from which a hypogynous flower is supposed to descend by condensation, according to the classical view of evolution of the flower. Occasional findings in the last decades of crushed flowers of Tertiary age, even if their affinity is problematic, continue to add to the impressive record of the presence of numerous cyclic flowers in this geological period.

The identification of fossil herbaceous seeds is different for other reasons besides distortion and partial destruction of their fossilized remains, when in flattened state of preservation. Even when their form is intact and all details are perfectly preserved, their identification is handicapped by the lack of organized knowledge of the essential details in the living herbaceous seeds. Only recently have seeds of various weeds been subjected to detailed study and illustrated in the Seed Laboratory of the U. S. Dept. of Agriculture, thanks to the initiative of the late Professor F. H. Hilman. When published, the illustrations of these seeds will furnish an important starting point in the identification of herbaceous fossil seeds, which should be followed by comprehensive comparative study with living seeds from herbaria, or from systematic seed collections, or both.

Because of this lack of organized knowledge of living herbaceous seeds, Cenozoic fossil seeds usually are only generally compared with the seeds of herbs now living in the general vicinity of the geologic formations in which the fossils were collected; this rather unscientific "short-cut" method results in nearly as many disastrous errors as the identifications attempted. Unfortunately, these errors crept in various scientific summaries and popular

accounts, and now it is difficult to "weed" them out. The history of some erroneous identifications is appended to this paper.

Of the fossil herbaceous seeds collected in Europe only a few are not flattened and are sufficiently preserved for reliable identification. Nutlets of *Lithospermum* from Pleistocene, achenes of sedges, and seeds of water-soldier (*Stratiotes*) from the Tertiary and Pleistocene, are among the best known cases of correctly identified seeds from Europe. The work on *Stratiotes* was particularly successful and important, because both the outer and inner structures of these stony seeds are usually preserved. The excellent research and summary by Chandler (1923) of all known fossil material of these monocotyledonous seeds greatly advanced our knowledge of their evolution throughout the Cenozoic; they do not show any changes greater than specific ones since their first known appearance in the Eocene of Europe.

Unlike the somewhat persistent, though erroneous identifications of *Lithospermum* in the Tertiary of the New World, the identification of this genus from the European Pleistocene is quite correct, and so is probably its unillustrated record in the American Pleistocene. The already mentioned Myosotis-like flower, and some seeds identified by Heer as borages, establish the presence of herbaceous representatives of the family in the late European Tertiary, but generic identifications of these remains, by necessity, indicate only broad affinities with the family. On the contrary, because of the superb degree of preservation and abundance, the fossil seeds of borages and grasses which are found in the late Tertiary of the Northern MidContinent, can be treated taxonomically with almost as much confidence as their living relatives, because to considerable extent, the latter, too, are taxonomically differentiated on the basis of their seeds.

Well preserved fossil seeds of herbaceous borages, which are quite unlike those of *Cordia*, the only living and fossil arboreal genus of the family, are identified by their shape, sculpture, and the characteristics of the scar of attachment. The shape of nutlets is, to some extent, influenced by their position in a fruit; a cycle of four nutlets is attached symmetrically around a common style, and the nutlets are adpressed to each other by their side. The fossil nutlets are either symmetrical near the central plane (in fossil and living *Cryptanthe* or *Krynitzkia*), or depart from this symmetry, perhaps because of differential pressure in the course of early growth, which results in the development of an equal number (two and two) of dextral and sinistral nutlets (in fossil *Biorbia* and living *Anchusa*, and others).

Contrary to the existing opinion that *Lithospermum* with smooth nutlets is a genus ancestral to related living genera with corrugated nutlets, the fossil record seems to indicate the development of living *Lithospermum* (with smooth nutlets) and of *Anchusa* (with very corrugated nutlets) from the genus *Biorbia*, apparently ancestral to both of them, whose nutlets are slightly to moderately corrugated. Species with nutlets intermediate between *Biorbia* and *Anchusa*, and between *Biorbia* and *Lithospermum* have been found in the upper Pliocene of the High Plains. These forms are shown in their respective stratigraphic and phyletic position in Pl. 1. figures 2-5. It seems possible that an unknown lower Pliocene form ancestral to *Biorba* possessed nutlets that were smooth, as theoretically postulated by Johnston, but it is not likely that such

provisional smooth-sided nutlets, when discovered, will resemble the nutlets of living *Lithospermum*.

The protective covers of seeds of fossil grasses, generally called hulls and made up of the hard parts of their florets, are usually well preserved in fossilization. They are made of two hard glumes: lemma and palea, the edges of the latter being overlapped by the edges of the former. Hulls are symmetrical about the plane which is median in both lemma and palea. The lemma has several longitudinal veins, which are visible as ribs or keels of varying prominence, while the palea invariably contains only two veins, which are usually not very prominent. The characteristics of the scar of attachment, and the development of callus, awns, cusps, tubercles, hair, and other sculptural details provide other characters on which the taxonomy of seeds is based in both generic and specific delimitation. Additional help can be derived also from the pattern of the epidermis, as indicated by extensive histological study of grass epidermis by Prat (1932).

Because fossil seeds are so abundant and are found throughout the geological sequence of the late Tertiary sediments in the High Plains to the Mid-Continent, it was possible, by extensive and repeated collecting, to construct an accurate and reasonably complete record of development of that part of the prairie vegetation, whose protective seed covers were fossilized in the rocks.

The most complete evolutionary record is furnished by the collected hulls of Stipeae (Plate 1, figures 6, 7). It proved the taxonomic integrity of the Stipeae as a tribe independent of the Agrostidae, thus supporting the contention of Hitchcock and other taxonomists, who regarded the old tribe Agrostidae as an artificial mixture of grasses belonging to more than one tribe. The record of fossil grasses from the High Plains discloses the development of all known genera of the tribe Stipeae, including the living Mexican-Central American-South American genera *Piptochaetium* and *Nassella*. The earliest Stipeae were collected from the lower Miocene rocks (Arikaree and higher). The apparent single ancestral form is small, but already possesses the essential characters of the hull of the living Stipeae: cylindrical form; well developed callus, sharpened at the end by the acutely inclined scar of attachment; tuberculate and pubescent epidermis on both lemma and palea; and a scar at the apex for apparent attachment of an awn, though the latter has not been found preserved on any of these fossil hulls. The rapid evolution of the Stipeae is expressed by differentiation in size, shape, and epidermal sculpture; reduction of the palea, and of some parts and their details: callus, tuberculation, pubescence, and others; and by the development of devices for better protection of the grain (caryopsis) from desiccation, such as interlocking of the lemma in the palea; rolling of the lemma in cigar-like fashion, and by the improvement of means for dispersal and for burial of seeds, such as stiffening of the awn, its hygroscopic twisting, and plumage; the latter feature apparently developed only late in Pliocene or in Pleistocene. The genetic differentiation of the Stipeae apparently was many times as rapid as that in contemporaneous arboreal vegetation, whether the differentiation be judged by observation of changes in leaves, or in seeds. For instance, stones of hackberry, which are as abundant and well preserved as hulls of Stipeae in most zones of the late Tertiary rocks in the High Plains, show no change throughout Miocene, Plio-

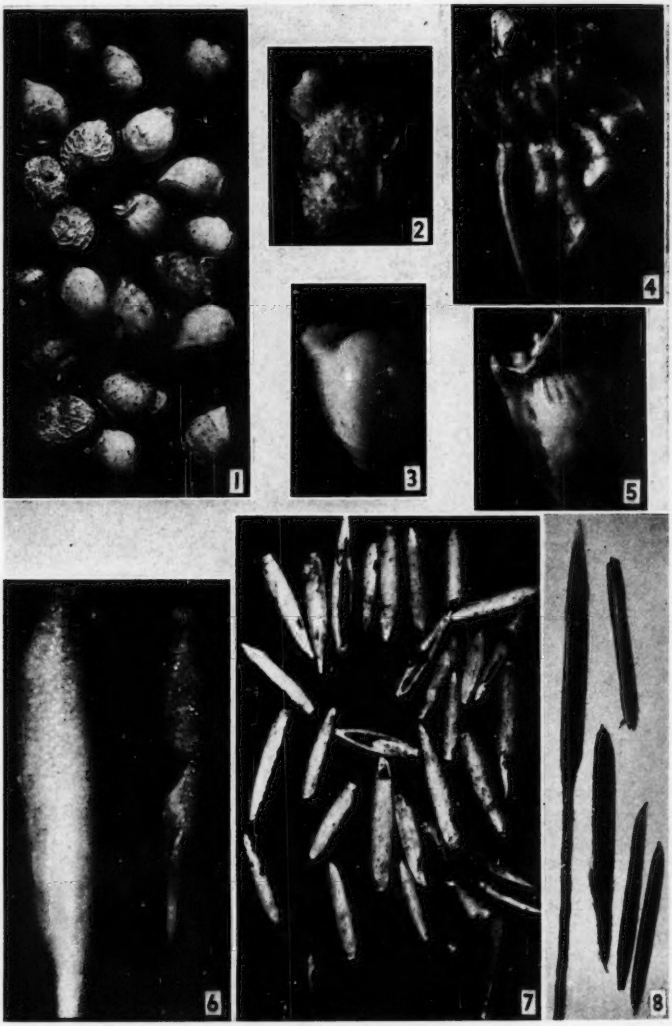

PLATE 1.—Tertiary and living herbaceous seeds. Figs. 1 to 5. Nutlets of Boraginaceae. 1. *Biorbia fossilia* (Berry) Elias. Middle Pliocene. Mixture of corrugated and non-corrugated nutlets in a single sample. Dextral anl sinistral nutlets recognizable among both kinds. ×4. 2. *Biorbia* n. sp. Uper Pliocene, near Chalkie, Oklahoma, collected by J. W. Stovall. ×10. 3. *Prolithospermum johnstoni* Elias. Upper Pliocene, near Sharon

cene and Recent, and only the hackberry stones from the Oligocene in the same region can be classified in a different species. The well known similarity of most Tertiary and even Cretaceous angiospermous arboreal leaves with those of living species, and the ensuing difficulty in differentiating fossil from living species, also seems to indicate a slow differentiation of angiospermous trees. On the other hand, the fossil record discloses a succession of numerous species and the origin of new genera of Stipeae in the course of Miocene and Pliocene times.

Likewise herbs of Borages and of *Crepis* (as analyzed by Babcock, whose conclusions are supported by the fossil record) went through a comparatively rapid genetic differentiation in late Tertiary time.

Corrections of Erroneous Identifications of Some Tertiary Seeds, and Other Identifications in Need of Revision

Osborn in his book Age of Mammals (1910, p. 342) cites the presence of fossil *Tithymalus* (*Euphorbia*) in the Tertiary rocks of the Mid West on the authority of T. D. A. Cockerell (1909, 1914). But it was proved by E. W. Berry (1928) that the fossil seeds in question do not belong to *Euphorbia*, a herb, but to hackberry, a tree, unrelated to *Euphorbia*. However, the correct identification of the same kind of seeds from the same area as hackberry was made in 1876 by Henry Engelmann, a geologist and naturalist of the U. S. Survey of Territories, and later by Professor E. H. Barbour (1925) of the University of Nebraska. These contributions apparently were overlooked by Cockerell and Berry.

In 1928 E. W. Berry identified three species of well preserved Tertiary seeds from Kansas as *Lithospermum*, a common borage herb now growing in the American prairies. However, none of them belong to *Lithospermum*, rather two of these are grass seeds, which were oriented by Berry in an up-side-down position, that made them look somewhat like the seeds of living *Lithospermum*. Even after their true nature as grass seeds was recognized (Elias, 1932) it took some time before it was realized that Berry's original orientation was incorrect and should be reversed. As soon as this was done (Elias, 1935), the classification of these seeds in the living grass tribes was relatively easy. Their closest relatives were found among forms now living in North and South America: *Stipa*, *Piptochaetium* and others.

The original classification of the third species of Berry's three seeds with *Lithospermum* was justly criticized by Betty Watt Brooks (1928), but her identification of the species as a small variety of hackberry was likewise incorrect. She gracefully admitted (in a personal communication) the error in classification, and agreed with the conclusion that the seeds belong to a peculiar borage (*Biorba* Elias), which stands closest to the European *Anchusa* and its relatives, and is apparently ancestral to the European Anchuseae, as well as to the cosmopolitan *Lithospermum*.

As can be seen from this review, the final, correct identification of the American fossil seeds discussed above could be accomplished only after detailed comparison not only with species growing in North America, but also with species from the Old World and South America. The fact that one of them (*Biorba*) is closer to some European than to living American borages should not be very surprising in view of the fact that horses, camels and many other mammals, which originated in North America, migrated

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Springs, Kansas. ×10. 4. *Lithospermum linearifolium* Goldie. Recent, from Panhandle of Texas. ×10. 5. *Anchusa aegyptiaca* (L.) DC. Recent, near Jerusalem. ×10.

Figs. 6-8. Hulls of Stipeae. 6. *Stipidium schereri* Elias. Lower Miocene, near Dunlap, Nebraska. The earliest known species of the tribe Stipeae. ×20. 7. *Stipidium commune* Elias, Lower Pliocene, near Valentine, Nebraska. ×4. 8. *Stipa spartea Trinius*. Recent, northern Mid-Continent of N. America. On left side hull in up-side-down position, with twisted awn attached; in lower center hull without awn (which is broken off); on right side detached paleas. ×4. (Scale slightly smaller than indicated.)

and survived elsewhere till the present, but became extinct in the country of their origin, where they were reintroduced by man.

The following story of another misidentification is equally instructive. In a stimulating sketch of the principles of Paleoecology, Clements (1918) speaks about the presence of fossil *Stipa*, a speargrass, in the rocks of the Tertiary Florissant Lake in Colorado without reference to its original authority. When describing the remains of a Stipa-like grass from the late Tertiary of the High Plains in Kansas and Colorado (Elias, 1932), I was not aware of the alleged preesnce of a fossil *Stipa* in the Tertiary flora of Florissant, Colorado, and Dr. Cockerell called my attention to this record (Cockerell 1908, p. 79; see also Knowlton 1919, p. 612). In answer to my subsequent query, Clements admitted that he quoted the presence of *Stipa* in the Florissant Tertiary rocks on the authority of Cockerell's identification. In view of all this I felt obliged to accept the identification. Because at that time (1936) the phylogenetic history of the Tertiary Stipeae had been completed, it seemed justifiable to find a place for "*Stipa laminarum*" in the determined phylogenetic sequence. According to it, the known *Stipeae* appear in the early Miocene with seeds carrying fairly long, sharp calli, but by the middle of the Pliocene some species had suffered considerable reduction and even complete suppression of calli. Because "*Stipa laminarum*" (photographs in Cockerell, 1908, Pl. 6, figs. 1, 3; also Elias, 1942, Pl. 4, figs. 3, 4) has a very short callus (or practically none), it seemed that the Florissant Lake beds, where "*Stipa laminarum*" belongs, must certainly be younger than Oligocene or Early Miocene, to which time they are usually referred (Gazin, 1935; MacGinitie, 1937). This view was expressed in a joint paper with Chaney (1938, p. 18), and repeated in an oral remark following the presentation by MacGinitie of his comprehensive paper (1937). However, I was still dissatisfied with my own conclusion, and finally decided to request the types of "*Stipa laminarum*" for examination. Upon critical examination, it was found that these remains do not belong to *Stipa* or to the Stipeae, and it is still uncertain that they belong to a grass (Elias, 1942, pp. 103-105, Pl. 4, figs. 3, 4). Thus the previous conclusions regarding the probable place of the species *laminarum* in the phyletic sequence of the Stipeae are no longer tenable, while the original interpretation of the evolution of the tribe Stipeae, as based on the fossil record from the High Plains, remains valid. That is, the absence of a callus in "*Stipa laminarum*," now renamed *Clementsiella laminarum* (Elias, 1942, p. 103), is no longer indicative of the age of the Florissant Lake beds. Their age should be judged solely on the evidence of the other fossil plants (MacGinitie, 1937), and animals (Gazin, 1935).

While discussing these cases with Mrs. Agnes Chase, of the U. S. National Herbarium, we also considered Knowlton's reference to her authority of the identification of *Muhlenbergia*, a grass of the tribe *Agrostidae*, from the same Tertiary Florissant Lake (Knowlton, 1916, p. 250, Pl. 13, figs. 1-3); she disclaims responsibility for this identification and agrees, that while the remains in question may belong to a grass, as originally suggested, they certainly should not be classified with *Muhlenbergia*.

As far as can be judged from published illustrations and descriptions, the following identifications of Tertiary herbaceous remains in America are also doubtful and need critical study.

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PHALARIS ? GEOMETRORUM, Cockerell, T. D. S., 1913. Fossil flowers and fruits (III), Torreya, vol. 13, p. 76, fig. 2.

YUCCA sp., aff. ALOIFOLIA Linné, Berry, E. W. 1917. (The) Flora of the Citronella formation. U. S. Geol. Survey Prof. Pap. 98-I, p. 194 and 197, Pl. 45, fig. 7.

FESTUCA sp., Berry, E. W., 1917. Fossil plants from Bolivia and their bearing upon Eastern Andes. U. S. Nat. Mus., Pr., vol. 54, p. 121-222, Pl. 15, figs. 3-4.

Apparently in view of the repeated failures in the past to establish a scientifically valid record of fossil mesic and xeric grasses and other herbs, a general skeptical attitude toward studies of these remains prevailed in some authoritative paleobotanical circles. For instance, in recent comprehensive summaries of the fossil floras of the world,

such as Seward's *Plant Life Through the Ages*, and in special treatises dedicated to grasses and their natural history, such as *The Gramineae* by Agnes Arber, fossil grasses and other herbs are neither dsicussed nor mentioned. This is a tacit admission that our knowledge of the fossil representatives of these herbaceous plants was so imperfect and inconclusive, that it was best to omit it entirely from the record and from the discussions.

The Russian botanist Komarov, in a popular account on the *Origin of Plants*, goes so far as to say that "meadow and prairie grasses left no traces of their existence in the Tertiary," and that "one may think that meadows and prairies did not exist at all in Tertiary time." This view is of course repudiated by the discovery of the prolific late Tertiary prairie grasses from the High Plains of America.

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NEBRASKA GEOLOGICAL SURVEY,
LINCOLN, NEBRASKA.

A Revision of Phacelia Sect. Euglypta

John Thomas Howell

Introduction

Phacelia sect. *Euglypta* consists of a small group of annual species in which the seeds are transversely wrinkled or corrugated and the corollas early deciduous. The two first-named species, *Eutoca Cumingii* of South America and *Eutoca brachyloba* of California, were placed by Bentham (1835, pp. 276, 277) in the genus *Eutoca* R. Br. because of the numerous seeds in the capsules. In 1845 *Eutoca Cumingii* was made the type of the genus *Microgenetes* by Alphonse de Candolle (1845, p. 292), a genus separated from *Eutoca* on the absence of corolla-scales and from *Cosmanthus* Nolte on variations in placentation and corolla. In 1871 Sereno Watson described the section *Euglypta* (1871, p. 254) and referred to it the five species with transversely corrugated seeds named by Torrey from collections made on the expeditions of Ives and of King to western America. Four years later Gray (1875, p. 326) adopted *Microgenetes* as the sectional name for the group (which also then included *P. micrantha* Torr., now referable to *Ellisia* or *Eucrypta*), and placed Watson's name in synonymy. Brand in his monograph of *Hydrophyllaceae* (1913) accepted Gray's name for the section, although according to the International Rules Watson's name should have been used since it had clear priority. In 1917 Rydberg (1917, p. 702) used the sectional name *Bicolores* to designate those speices of the group which he was treating. Jepson in 1925 (p. 818) named the group as subgenus *Microgenetes*. Since the group seems best treated as a section in the rather closely knit genus *Phacelia*, I am here restoring Watson's long-suppressed sectional name.

Section *Euglypta* is closely related to sect. *Miltitzia*, a western North American group in which the seeds are also transversely rugose but in which the corollas are persistent even in fruit. These two sections have probably been derived from the North American section *Eutoca* but it is not clearly evident just where the sections approach each other most closely. In habit and in foliage there is a notable resemblance between *P. Fremontii* Torr. and *P. Douglasii* (Benth.) Torr. and, although the markedly different fruits of the two would seem to preclude a close relationship, a critical study of *P. Douglasii* has disclosed that in certain variants the pits on the seeds tend to be arranged in transverse rows (Howell, 1945b, p. 471). In the character of the fruit, species of sections *Euglypta* and *Miltitzia* are much more like the species of sect. *Eutoca* related to *P. pulchella* Gray and even the rather remarkable habits of the plants of these different groups closely simulate each other. It may be that the definite morphologic clues to the interrelationship between these groups have been lost but it is hoped that with further study a clearer understanding of their phylogeny may be reached.

In the present study, twelve species are recognized in the section, eleven

in western North America and one in Chile and Argentina. The South American species, *P. Cumingii,* is remarkable for its altitudinal range, occurring from near sea level to high in the Andes at over 12,000 feet (4,000 m.). With the exception of *P. brachyloba* all are restricted to arid habitats which vary from desert flats and slopes to high dry plains and desert mountains. The North American species are particularly common in the Great Basin between the Cascade-Sierran crest and the Rocky Mts., although in California, *P. Fremontii,* one of the desert species, ranges a short distance west of the Sierran crest. In the same state, *P. brachyloba* is nearly restricted to the Pacific coastal drainage where it frequently extends upward to the lower part of the main forest belt in relatively moist habitats.

The species are closely related and, although most are adequately distinct, they are frequently separable only on the basis of rather technical characters. Although the marked differences in the sizes of the corollas of certain of the species offer a convenient way for distinguishing them in a key, it would seem that the relationship between species cuts directly across the corolla-size in a notable way. Thus large-flowered *P. Fremontii* seems most closely related to small-flowered *P. affinis,* large-flowered *P. bicolor* and *P. Leibergii* to small-flowered *P. glandulifera,* and large-flowered *P. calthifolia* to small-flowered *P. pachyphylla.* Several of the species, such as *P. Cumingii, P. Fremontii,* and *P. Ivesiana,* exhibit a considerable amount of variability which is presumably due to small genetic differences within the specific complexes. On the other hand, even such relatively stable species as *P. glandulifera, P. pachyphylla,* and *P. neglecta* are frequently diverse in appearance but the variations shown by these species seem chiefly due to edaphic or climatic causes.

ACKNOWLEDGMENTS

Although I have been privileged to study in the field all the species treated in this revision except the South American *P. Cumingii* and the Oregonian *P. Leibergii,* I would not have been able to complete my work without the cooperation I have received from many botanists and institutions. During the course of my study which has been pursued in the Department of Botany of the California Academy of Sciences, I have examined over a thousand collections, most of which have been generously loaned to me from twenty-two different herbaria. Specimens from the various herbaria are cited as follows:

California Academy of Sciences (CAS)
Chicago Natural History Museum (CM)
Dudley Herbarium, Stanford University (DS)
Frank Peirson, Altadena, California (FP)
Gray Herbarium, Harvard University (G)
Intermountain Herbarium, Utah State Agricultural College (IM)
Missouri Botanical Garden (M)
Greene Herbarium, University of Notre Dame (ND)
New York Botanical Garden (NY)
Pomona College (P)
Rocky Mountain Herbarium, University of Wyoming (RM)
H. D. Ripley and R. C. Barneby (RB)
Rancho Santa Ana Botanic Garden (RSA)
United States Field Station, Sacaton (S)
University of Arizona (UA)
University of California (UC)
University of Idaho, Southern Branch (UI)
University of Nevada (UN)
United States National Herbarium (US)
University of Utah (UU)
University of Washington (UW)
Willamette University (W)
Washington State College (WS)

I am very grateful to the curators of these collections for making them available to me. Also I wish to express my special gratitude to Miss Alice Eastwood through whose interest and generosity I have been able to travel so widely afield through the western United States during the past decade.

PHACELIA sect. EUGLYPTA Wats.,
Bot. U. S. Explor. 40th Paral. (King's Exped.) 254 (1871)

Microgenetes A. DC. in DC. Prodr. **9**:292 (1845).
Phacelia sect. *Microgenetes* (A. DC.) Gray, Proc. Amer. Acad. **10**:326 (1875).
Phacelia subsect. *Microgenetes vera* Gray, ibid., 327.
Phacelia sect. *Bicolores* Rydb. Fl. Rky. Mts. & Adj. Plains 702 (1917).
Phacelia subgen. *Microgenetes* (A. DC.) Jepson Man. Fl. Pl. Calif. 818 (1925).

Flowers 5-merous; corolla deciduous, tubular-campanulate to funnelform-campanulate or subrotate, the limb white, lavender, bluish, violet, or reddish-violet; corolla-scales present or lacking; filaments glabrous or hairy; ovary more or less pubescent and sometimes glandular, style hairy at base or above, ovules 8-114; capsule obtuse to subacute, apiculate or muticous; seeds transversely corrugated. —Annual herbs chiefly characteristic of desert plains and mountains in western North America and in South America in Chile and Argentina; stems and leaves variously pubescent and usually glandular; leaves oblongish or roundish, entire or shallowly crenate to pinnately or bipinnately parted or divided.

KEY TO THE SPECIES

A. Leaves mostly elongate, oblong to ovate, the lower leaves pinnately serrate to divided, the lobes or divisions sometimes again toothed, lobed, or pinnatifid (or the leaves sometimes entire or subentire in *P. gymnoclada* or *P. brachyloba*), the base of the blade generally cuneately narrowed; calyx-divisions mostly longer than the capsule; capsules generally oblongish, not globose-turgid; ovules 8-43 (or rarely to 53 in *P. brachyloba*).

B. Corolla inconspicuous, 2.5-6.5 mm. long (see also *P. gymnoclada* with corolla 6-10 mm. long).

C. Racemes usually well projected above the leafy part of the plant; calyx-divisions in fruit narrowly to broadly spatulate; stamens attached at or very near the base of the corolla.

D. Corolla cylindric-tubular; stamens included in corolla-tube, the filaments broadened and flattened at base; nonglandular hairs on lower part of stem mostly spreading ..... 1. *P. Cumingii*

D. Corolla tubular-campanulate; stamens equaling or a little exceeding the corolla-throat, filaments not broadened; nonglandular hairs on lower part of stem usually retrorse (except in var. *patens*) ..... 2. *P. affinis*

C. Racemes not projected above the leafy part of the plant; calyx-divisions in fruit linear to oblanceolate, rarely spatulate; stamens attached well above base of corolla.

E. Glands on stems usually minute; corolla 2.5-4 mm. long, limb white; corolla-scales free from filaments or obsolete; filaments glabrous ..... 6. *P. Ivesiana*

E. Glands on stems capitate and conspicuous; corolla 4-6.5 mm. long, limb lavender; corolla-scales united to base of filaments; filaments more or less hairy ..... 7. *P. glandulifera*

B. Corolla conspicuous, 7-17 mm. long (or rarely only 6 mm. long in *P. gymnoclada*).

F. Leaves deeply lobed or divided to bipinnatifid, or if rarely shallowly lobed or subentire (as in *P. brachyloba*) then the stems erect and simple at the base and the seeds only 0.6-1 mm. long.

G. Racemes usually well projected above the leafy part of the plant; stamens attached at or near base of corolla, filaments glabrous (except sometimes in *P. Fremontii*).

H. Primary stems usually much condensed; corolla-scales present, attached at base to the filaments; seeds 1-1.5 mm. long ..... 3. *P. Fremontii*

H. Primary stems elongate; corolla-scales present or lacking, if present free from the filaments; seeds 0.6-1 mm. long ..... 4. *P. brachyloba*

G. Racemes not projected above the leafy part of the plant; stamens usually attached well above the base of the corolla, filaments hairy (rarely glabrous in *P. bicolor*).

I. Corolla funnelform-campanulate; corolla-scales attached to the filaments 1.5-3 mm.; stamens included in the corolla-tube; style and branches 3-6 mm. long ..... 8. *P. bicolor*

I. Corolla elongate-campanulate; corolla-scales attached to the filaments 0.5-1 mm.; stamens equaling or exceeding the corolla-throat; style and branches 5-8 mm. long ..... 9. *P. Leibergii*

F. Leaves shallowly lobed or merely serrate or entire; stems branching widely from the base, sparsely leafy; seeds 1-1.75 mm. long ..... 5. *P. gymnoclada*

A. Leaves broad and generally roundish, serrulate or crenulate, the base of the blade usually truncate or cordate; calyx-divisions mostly equaling or shorter than the capsule; capsules subglobose-turgid; ovules 48-114.

J. Racemes not projected above leafy part of plant; corolla whitish or pinkish, inside of corolla-throat glabrous; anthers yellow ..... 10. *P. neglecta*

J. Racemes well projected above leafy part of plant; corolla violet to purple, inside of throat pubescent; anthers lavender.

K. Corolla small, 5-6.5 mm. long ..... 11. *P. pachyphylla*

K. Corolla larger, 8-12 mm. long ..... 12. *P. calthifolia*

1. PHACELIA CUMINGII (Benth.) Gray Proc. Amer. Acad. 10: 327 (1875)

Eutoca Cumingii Benth., Trans. Linn. Soc. **17**:276 (1835).
Microgenetes Cumingii (Benth.) A. DC. in DC. Prodr. **9**:293 (1845).
Eutoca frigida Phil. Florul. Atacam. 37 (1860).
Eutoca pusilla Phil., Linnaea **33**:186 (1864-5).
Eutoca pinnatifida Phil., Anal. Univ. Chile 189 (1870).
Eutoca grandis Phil., Anal. Univ. Chile **90**:226 (1895).
Eutoca Peraltae Phil., ibid., 227.
Eutoca litoralis Phil., ibid., 228.
Phacelia Cumingii (Benth.) Gray var. *pusilla* (Phil.) Reiche Fl. Chile **5**:163 (1910).
Phacelia Cumingii (Benth.) Gray var. *litoralis* (Phil.) Reiche, ibid., 164.
Phacelia Cumingii (Benth.) Gray var. *grandis* (Phil.) Reiche, l. c.
Phacelia frigida (Phil.) Reiche, l. c. Not *P. frigida* Greene. Pitt. **4**:39 (1899).
Phacelia Cumingii (Benth.) Gray var. *frigida* (Phil.) Brand, Das Pflanzenr. IV. 251: 125 (1913).

In this list I have omitted the name of *Eutoca lomarifolia* Phil. (Anal. Mus. Nac. Chile 54, —1891) which was treated as a synonym of *P. Cumingii* "ex parte" by Brand (1913, p. 125). The Philippi specimen of *E. lomarifolia* from Tarapacá in U. S. Nat. Herb. is *P. nana* Wedd.

Root annual; stems diffusely spreading to substrictly erect, sometimes simple below and branched above, usually with several branches at or near the base with the chief branches curving outward a little below, stems 0.4 - 3.3 dm. long, capitate-glandular and hirsutulous from the base, the nonglandular hairs spreading, the stalks of the glands translucent and shining; leaves mostly loosely rosulate near the base, the cauline leaves few, sparse, and smaller, the blades oblongish to ovate-lanceolate or ovate, 1-3 cm. long, 0.5 - 1 cm. wide, pinnately lobed with broad rhachis varying to bipinnatifid with the divisions rather discrete and extending nearly from the midrib, the lobes or divisions lobed, toothed, or entire, the larger divisions frequently alternating with much smaller segments, hirsutulous and more or less glandular above and below, the petioles 1 to nearly 2 cm. long below, much shorter or nearly lacking above; racemes solitary or several, usually at the ends of the leafy-bracteate pedunclelike stems and mostly well projected above the leafy part of the plant, sessile or shortly pedunculate, the primary inflorescence usually represented at or near base of plant by a single flower, pedicels usually 1-4 mm. long, erect or the lowest spreading or reflexed; calyx-divisions in flower 3-5 mm. long, in fruit 4-10 mm. long, 1-3 mm. wide, narrowly oblanceolate to strongly oblanceolate-spatulate, obtuse, hirsutulous and densely glandular, tending to be 3-nerved at base and venulose above; corolla tubular, limb lavender to violet and tube yellowish or violet, 4.5-6 mm. long or rarely smaller, lobes 1 mm. long, spreading; corolla-scales very narrow and scarcely evident or entirely lacking; stamens attached very near base of corolla, included in the corolla-tube, unequal, 2-3 mm. long, filaments glabrous, anthers 0.25 mm. long; style and branches 1-2 mm. long, style sparsely hairy to the middle, branches 0.25-0.5 mm. long; ovary 1 mm. long, glabrous below, hirsutulous above, ovules 15-25; capsule oblong to globose, usually thinly chartaceous, 3-7 mm. long, 2-3 mm. wide, obtuse or a little emarginate, sparsely hirsutulous above, apiculation broad and evident or obsolete; seeds 1-1.75 mm. long, oblong to ovate, obtuse, or subobtuse or acute at one end, corrugations 6-8, mostly rather low and broad.

Gravelly soil of rocky slopes and ledges or frequently in sandy soil of stream-beds and valley lands, from sea level to over 12,000 feet (4,000 m.): in Chile from Tarapacá south to Santiago and in Argentina in the provinces of San Juan, Mendoza, Chubut, and Santa Cruz.

Representative collections: CHILE: Cerro de la Copa, Antofagasta, *Werdermann No. 1042* (CAS, G, UC, US); Atacama, *Philippi* (US); Cordillera Rio Turbio, Atacama, *Werdermann No. 939* (CAS, G, UC); Sierra San Miguel, Atacama, *Johnston No. 4907* (G, US); Coquimbo, *Philippi* (US, "*Eutoca pinnatifida* Ph."), *Philippi* (Us, "*Eutoca grandis* Ph."); Baños del Toro, Coquimbo, *Werdermann No. 204* (CAS, G, UC, US); Rivadavia, Coquimbo, *Werdermann No. 97* (CAS, G, UC); east of Santiago, Santiago, *Pirion No. 474* (G).

ARGENTINA: Cordillera de la Ortiga, San Juan, *Johnston No. 6178* (G, US); Cajon Ginebra Chico, Chubut, *Everdam, Beetle & Grondona No. 24547* (G, UC); Las Heras, Santa Cruz, *Donat No. 133* (CAS, G, UC); Minerales, Santa Cruz, *Donat No. 192* (CAS, G, UC).

Phacelia Cumingii is both widespread and variable, but, although I have had a considerable series of South American specimens available for study, I have not found it possible to recognize more than one species because of

intergradation between even the most outstanding variations; and, without a thorough and critical knowledge of Philippi's numerous specific segregates, I do not believe it proper to recognize named varieties. From my study of the North American species, I expect that the complex may ultimately be divided but, to do it properly, one must have a more intimate knowledge of the plants as they grow and of the places where they grow than can be obtained from herbarium specimens alone. Hence, in the above listing of the names which are involved in this complex, I do it not so much in the manner of straight forward synonymy as in a highly tentative way to be realigned as further study may warrant.

The most interesting fact disclosed by my study of *P. Cumingii* is its close connection to the North American species, an affinity scarcely to be expected when one considers the wide separation between the northern and southern parts of the section. Asa Gray (1878, p. 169) related *P. Cumingii* to *P. Ivesiana* and, from the order of species in the treatment by Brand (1913, p. 125), one would infer the same relationship. My studies, however, indicate that *P. Cumingii* is very closely related to *P. affinis* and that they are separable only on rather meager characters.

De Candolle (1845, p. 293), Gray (1875, p. 327), and Brand (1913, p. 124) have emphasized the absence of corolla-scales in *P. Cumingii;* and, although the scales are generally absent in *P. Cumingii* and present in *P. affinis,* occasionally they are lacking in the latter and rarely they are represented by very narrow processes in the former. The most significant difference between the two would seem to be in the shape of the corolla which is cylindric-tubular with narrow limb in *P. Cumingii* but tubular-campanulate with a relatively broader limb in *P. affinis.* Also there is a tendency for the corollas in *P. Cumingii* to be longer (4.5-6 mm.) than in *P. affinis* (3-5 mm.). In *P. Cumingii* the stamens are included in the more elongate corolla-tube while in *P. affinis* the longer stamens usually equal the ampliate throat or slightly exceed it. The filaments in *P. affinis* are round and slender even at the base but in *P. Cumingii* the filaments are noticeably broadened and flattened near the point of insertion. The seeds of *P. affinis* are mostly 0.75-1 mm. long (one collection 1-1.25 mm. long), while in *P. Cumingii* the seeds are mostly 1-1.75 mm. long. The aspect of the plants is frequently confusingly similar, although in *P. affinis* the stems and inflorescences are generally more slender and the upper flowers are not always so congested, and usually *P. Cumingii* is markedly more glandular. In *P. Cumingii* the nonglandular hairs spread divaricately on all parts of the plant but in *P. affinis* the nonglandular hairs on the lower stems and on the petioles and rhachises of the lower leaves are commonly retrorse. Occasionally in *P. affinis* there are two kinds of nonglandular hairs, some spreading and some retrorse, and rarely, as in var. *patens,* the retrorse hairs are almost or quite lacking. As an easy mark for distinguishing these closely related entities, however, the character of the pubescence is an obvious and usually safe criterion.

Although the distinguishing characters between *P. Cumingii* and *P. affinis* may seem to be small and may frequently tend to overlap, the distinctions

assume truly specific significance when they are correlated with the distributional hiatus that is continental and hemispheric in magnitude. I believe there is no reason to question the specificity of the two entities.

2. PHACELIA AFFINIS Gray Syn. Fl. N. Amer. ed 2, 2: 417 (1886)

Plants annual with one to several erect or somewhat spreading stems from the base, 0.5-3 dm. tall, hirsutulous and more or less cinereous or glandular below, hirsutulous or puberulent and glandular above, the glandular hairs capitate with black heads and translucent shining stalks, the nonglandular hairs mostly white and opaque and on the lower part of the stem generally strongly reflexed; leaves chiefly on the lower part of the plant; the lowest leaves mostly rosulate, oblong-lanceolate, 1-4 cm. long, 0.5-1.2 cm. wide, pinnately divided to the midrib, the divisions oblongish or ovatish, entire, dentate or lobed, hirsutulous and sometimes cinereous, frequently capitate-glandular, the larger divisions frequently alternating with smaller segments, petioles to 4 cm. long, the nonglandular hairs on the petioles frequently retrorse, racemes elongate on slender peduncle-like, leafy-bracted stems, conspicuously exceeding the leafy part of the plant, the lowest flowers discrete with slender pedicels to 1 (or even 2) cm. long, the uppermost approximate with pedicels 1-2 mm. long, each plant usually with solitary flower near base; calyx-segments in flower 3-4 mm. long, 0.6-1.5 mm. wide, in fruit strongly accrescent, equal to markedly unequal, 6-10 mm. long, 1-2 mm. wide, narrowly to broadly oblanceolate-spatulate, hirsutulous and capitate-glandular, obtuse or subacute; corolla pale lavender or white with faintly yellowish tube, tubular-campanulate, 3-5 mm. long, the lobes 1-1.5 mm. long, the tube somewhat ampliate upward; corolla-scales linear, linear-filiform, or obsolete, 0.5-1 mm. long, free from the filaments; stamens 1.75-3 mm. long, attached at or very near the base of the corolla, filaments slender and glabrous, anthers 0.25-0.4 mm. long, oblong or roundish: style and branches 1-2 mm. long, the branches 0.2-0.5 mm. long, the style glabrous or hairy nearly to the branches; ovary about 1 mm. long, ovules 13-43, generally about 30; capsule oblong or elliptic, 4.5-5 mm. long, 2-2.5 mm. wide, subtruncately obtuse, apiculate, longitudinally sulcate, sparsely hirsute and glandular above, puberulent below, at base somewhat adnate to calyx; seeds plumply ovate to elliptic-oblong, obtuse, 0.75-1.25 mm. long, buff, the corrugations 6-8, thick and rounded.

As might be expected in a species ranging from middle Lower California to southwestern New Mexico and northern Nevada, *P. affinis* is rather variable, especially in habit and vestiture. Some plants that have evidently grown in shaded places have the leaves distributed along a simple erect stem, but generally several branches arise from the basal rosette and are almost leafless. Only in the isolated mountains of the Death Valley region of California and Nevada does a variant emerge that seems worthy of nomenclatural recognition. Whereas throughout the species the glandular hairs are most abundant in the inflorescence, in this variety the glandular hairs are numerous even to the base of the stems and the rosette leaves, and in addition the nonglandular hairs at the base of the stem are only occasionally retrorse. In the flowers and fruits small differences in the size of parts are also discernible.

KEY TO THE VARIETIES OF PHACELIA AFFINIS

Nonglandular hairs at base of stem retrorse; basal leaves not noticeably glandular; style and branches 1-1.6 mm. long ..... 2a. var. *typica*

Nonglandular hairs at base of stem mostly divaricately spreading; basal leaves glandular; style and branches 2 mm. long ..... 2b. var. *patens*

2a. **Phacelia affinis** Gray var. **typica,** nom. nov.

P. affinis Gray, l. c.

P. rugulosa Lemmon ex Greene, Pittonia **1**:175 (1888).

Stems slender or tending to be a little thickish, the nonglandular hairs at the base of the stems generally numerous and strongly reflexed; basal leaves not markedly, if at all, glandular; corolla 3-4.5 mm. long; style and branches 1-1.6 mm. long; capsule 5-5.5 mm. long.

Widely distributed but not common in sandy or gravelly soil of desert mountains from northeastern Nevada and adjacent Utah south to southwestern New Mexico and southern Arizona and west to southern California and middle Lower California (to about 27° N. Lat.).

Representative collections: CALIFORNIA: Tejon Pass, Kern Co., *Parish No. 9?16* (DS); Lockwood Valley, Ventura Co., *Hoffmann in 1930* (CAS, CM); Arraster Canyon, San Gabriel Mts. Los Angeles Co. (Fl. Calif. **3**:279); Byrnes Springs, San Bernardino Mts., San Bernardino Co., *Parish No. 3358* (CAS, DS, M, ND, NY, US); Palms to Pines Highway, 3400 ft., Riverside Co., *L. S. Rose No. 37125* (CAS, RSA, US); Jacumba, San Diego Co., *Abrams No. 3681* (CM, DS, G, M, NY, P); foot of Mountain Springs Grade, Imperial Co., *Peirson in 1927* (CAS); canyon above Keystone Spring, New York Mts., San Bernardino Co., *Munz No. 13721* (P).

LOWER CALIFORNIA: Northern Lower California, *Orcutt No. 1087* (G, type; UC, US); Lower California near boundary ("under bushes of manzanita near Ensenada" in Herb. Brandegee.), *Lemmon in 1888* (UC, type of *P. rugulosa* Lemmon); 9 miles southeast of Tecate, *Peirson No. 5829* (CAS, FP); Los Emes, Sierra San Pedro Martir, *Wiggins No. 9912* (DS); El Rancho Viejo, *T. S. Brandegee in 1889* (UC); 11 miles east of San Ignacio, *Wiggins No. 7904* (DS, UC).

NEVADA: East Humboldt Mts., Elko Co., *Watson in 1868* (US); Ely, White Pine Co., *Ripley & Barneby No. 3641* (CAS); Lehman Creek Canyon, Snake Range, White Pine Co., *Maguire No. 20813* (CAS, UC); Coyote Mts., Pershing or Lander Co., *Watson in 1868* (US); Currant Creek summit east of Currant, Nye Co., *Eastwood & Howell No. 9391* (CAS, WS); above Oak Springs, Belted Range, Nye Co., *Ripley & Barneby No. 3453* (CAS); Rocky Gap Spring, Charleston Mts., Clark Co., *Ripley & Barneby No. 3369* (CAS).

UTAH: Gold Hill, Tooele Co., *Jones in 1891* (P); Frisco, Beaver Co., *Jones in 1880* (P); southern Utah, *Palmer No. 3 in 1870* (NY, US); Beaver Dam Mts., Washington Co., *Eastwood & Howell No. 9071* (CAS, G, UU); Clear Creek Canyon, Zion National Park, Washington Co., *Eastwood & Howell No. 9218* (CAS); 5 miles east of Zion Park on road to Mt. Carmel, Kane Co., *Eastwood & Howell No. 9260* (CAS).

ARIZONA: Bright Angel Trail, Coconino Co., *Darrow in 1938* (UA); Iron Springs near Prescott, Yavapai Co., *Harrison No. 4005* (S); 2 miles east of Wickenburg, Maricopa Co., *Gillespie No. 5350* (DS, US); Mazatzal Mts., Gila Co., *Collom in 1935* (M, UA); Clifton, Greenlee Co., *Davidson in 1899* (DS); Baboquivari Mts., Pima Co., *Pringle in 1884* (CAS, G, M, NY, US); Tucson, Pima Co., *Thornber No. 4364* (CAS, UA); Canyon Diablo, Ajo Mts., Pima Co., *Kearney & Peebles No. 10823* (CM, US); mountains near Ruby, Santa Cruz Co., *Nelson & Nelson No. 1486* (M, NY, RM, UC, UW).

NEW MEXICO: Peloncillo Mts., Hidalgo Co., *Ripley & Barneby No. 4218a* (CAS).

2b. **Phacelia affinis** Gray var. **patens**, var. nov.

Herba erecta elegans caulibus gracilibus omnino dense glanduliferis usque ad basin, pilis eglandulosis basi caulis paucis et divaricate patentibus, raro reflexis; foliis basalibus glandulosis; corolla circa 5 mm. longa; stylo et ramis 2 mm. longis; capsula 4 mm. longa.

Occasional in desert mountains bordering or near Death Valley in California and Nevada, 8,000 to 10,000 feet.

Type: Herb. Calif. Acad. Sci. No. 188252, collected on rocky slope near summit of divide between Surprise and Hall canyons, 8500 ft., Panamint Mts., Inyo Co., California, *J. T. Howell No. 4037*, June 19, 1928. Isotypes are in the Dudley and Peirson herbaria.

Other collections: CALIFORNIA: Surprise Canyon above Panamint City, *Ferris No. 7937* (CAS, CM, DS, M, P, UC); Wild Rose Canyon, Panamint Mts., *Hoffmann No. 464* (CAS), *Munz No. 14827* (CAS, P); Crag Canyon, Grapevine Mts., Inyo Co., *Gilman No. 3256b* (P).

NEVADA: Cathedral Rock, 10,000 ft., Charleston Mts., Clark Co., *Jaeger in 1926* (P).

For a number of years this phacelia was regarded as *P. glandulifera* (cf. Howell, 1930, p. 5) or as *P. Ivesiana* var. *glandulifera* (cf. Munz, 1935, p. 412), but more recently Jepson (1943, p. 278) has included it in *P. Ivesiana* as indicated by a specimen cited from the Panamint Mts. Although the plants of var. *patens* seem to approach plants of *P. glandulifera* and *P. Ivesiana* in some minor details of habit and in the rather important character of the nonglandular hairs at the base of the stem, they are not unlike occasional slender plants that must be referred to *P. affinis*, and in the character of the glandular hairs with their shining translucent stalks, the Death Valley plants correspond exactly to *P. affinis*. Moreover the character of the staminal attachment, which I regard as critical and important in this group, is that of *P. affinis*. While some variations in the character of seeds are to be noted in *P. Ivesiana*, the seeds in var. *patens* are quite like those of *P. affinis* and differ more or less widely from the seeds of *P. Ivesiana* and *P. glandulifera*. Hence, these plants which have been referred heretofore to *P. glandulifera* or *P. Ivesiana* are treated as a variety of *P. affinis*.

3. PHACELIA FREMONTII Torr. in Ives' Colo. River Explor. Exped. Bot. 21 (1860)

P. Brannani Kell., Proc. Calif. Acad. Sci. **7**:90 (1877).
P. Hallii Brand, Beilage, Jahresb. Kgl. Gymnas. Sorau 8 (1911).

Annual herb, sometimes with an unpleasant odor; stems one to many from the base, 0.5-3 dm. long, erect or generally widely spreading, the lower part of the main stems frequently decumbent with the branches and inflorescences ascending or erect, the stems retrorsely hirsutulous below, becoming glandular above, the upper stems and inflorescences hirsutulous-puberulent and capitate-glandular; leaves mostly near the base, usually rather numerous in the basal rosette and much reduced and distantly scattered above, the flowering branches mostly well projected above the leafy part of the plant, leaves pinnately divi-

ded, the divisions usually coarse, oblong, ovate or roundish, entire or few-toothed, obtuse, rarely once or twice lobed with the ultimate segments rounded and bead-like, the chief divisions frequently alternating with smaller lobes or divisions, the entire blade narrowly oblong or elliptic, 0.5-5 cm. long, 1.5-20 mm. wide, the pubescence hirsutulous and frequently more or less scabrous, the hairs subappressed above and spreading below, more or less capitate-glandular especially below, petioles 0.5-3 cm. long, usually elongate, the flowers distant below, crowded above, pedicels 1-4 mm. long or rarely longer; calyx-segments in flower 4-6.5 mm. long, 0.5-2 mm. wide, in fruit 4-9 mm. long, 0.75-3 mm. wide, linear-oblong and linear-oblanceolate to oblong or oblanceolate-spatulate, subacute or obtuse, sparsely hirsutulous and densely glandular; corolla tubular-campanulate to funnelform-salverform, the tube campanulate, the limb usually ample and spreading, the corolla 7-17 mm. long, 4-20 mm. across, lobes 2-5 mm. long, the limb lavender to blue or violet or rarely white, the tube pale to deep yellow, sometimes with purplish spots or lines near the base; corolla-scales 2-4 mm. long, narrowly semi-elliptic, linear-attenuate above, attenuate below and attached to base of filaments for less than half their length, the free part of the scales usually conspicuous, usually widest well above the point of attachment to the filament; stamens inserted at the base of the corolla or a little above, unequal in length, 4-6 mm. long, filaments glabrous or rarely sparsely hairy near the base, usually flattened and widened towards the base, anthers 0.5-1.2 mm. long; style and branches 3.5-5.5 mm. long, the branches 0.5-1.3 mm. long, the style hairy to the middle or a little above; ovary 1 mm. long, ovules 12-43; capsule oblong, obtuse, apiculate or muticous, 5-6.5 mm. long, 2-2.75 mm. wide, sparsely hirsutulous and more or less glandular above, puberulent and sometimes viscidulous below; seeds oblong-ovate to ovate, angular, 1-1.5 mm. long, brown, usually rather coarsely corrugated, the corrugations 6-8 or rarely 10.

Slopes and flats in clayey or sandy soil in deserts and bounding ranges from southwestern Utah and northwestern Arizona west to southern Nevada and southern California, extending northward in the inner Coast Ranges to central California.

Representative collections: CALIFORNIA: California, *Frémont* (NY, type); Corral Hollow, San Joaquin Co., *Hoover No. 3032* (CAS); Merrill Valley, San Benito Co., *Hall No. 9901* (UC); Oil Canyon, Fresno Co., *J. T. Howell No. 5857* (CAS, CM, US); 14 miles north of Stratford, Kings Co., *J. T. Howell No. 5787* (CAS, US); 3 miles south of Blackwell's Corner, Kern Co., *J. T. Howell No. 5890* (CAS); near Soda Lake, Carisso Plains, San Luis Obispo Co., *Ripley & Barneby No. 3248* (RB); Frazier Borax Mine, Mt. Pinos, Ventura Co., *Abrams & McGregor No. 200* (CAS, DS, G); Cuyama Valley, Santa Barbara Co., *Munz No. 13620* (DS, P, UC); Caliente Creek, Tehachapi Mts., Kern Co., *Mason No. 5565* (UC); Greenhorn Mts., Kern Co. (Fl. Calif. 3:279); Walker Pass, Kern Co., *J. T. Howell No. 5002* (CAS, CM); Independence, Inyo Co., *Kerr in 1937* (CAS); Black Canyon, White Mts., Inyo Co., *Duran in 1930* (CAS, CM, DS, G, M, NY, P, RM, RSA, UA, UC, US); Great Falls Canyon, Argus Mts., Inyo Co., *Bailey & Robinson in 1930* (CAS, CM, M, UC, US); Wild Rose Canyon, Panamint Mts., Inyo Co., *J. T. Howell No. 3692* (CAS, DS); near Bradbury Well, Black Mts., Inyo Co., *J. T. Howell No. 3645* (CAS); Providence Mts., San Bernardino Co., *Hilend No. 374* (CAS); New York Mts., San Bernardino Co., *Alexander & Kellogg No. 1460* (CAS, UC); between Victorville and Barstow, San Bernardino Co., *J. T. Howell No. 3670*

(CAS); near Palmdale, Los Angeles Co., *Eastwood & Howell No. 3965* (CAS); Rock Creek, San Gabriel Mts., Los Angeles Co., *Peirson No. 163* (CAS); Swartout Canyon, San Gabriel Mts., Los Angeles or San Bernardino Co., *Hall No. 1264* (DS, NY, UC; type collection of *P. Hallii*); Cushenbury Grade, San Bernardino Mts., San Bernardino Co., *J. T. Howell No. 2706* (CAS); Quail Spring, Little San Bernardino Mts., San Bernardino Co., *J. T. Howell No. 3392* (CAS); Palms to Pines Highway, el. 3400 ft., Riverside Co., *L. S. Rose No. 37123* (CAS, NY).

NEVADA: Nine miles west of Lida, Esmeralda Co., *Keck No. 550* (CAS, DS, P, UC); Telluride, Nye Co., *Monnet No. 1167* (CAS); Mormon Mts., Lincoln Co., *Kennedy & Goodding No. 88* (CAS, DS, M, NY, UA, UC, US); Kyle Canyon Fan, Charleston Mts., Clark Co., *Clokey No. 7652* (CAS, CM, DS, G, M, NY, P, RM, UC, UN, US, UW, WS); Mica Spring, Clark Co., *Jones No. 5044* (CAS, M, NY, P, RM, UC, US).

UTAH: Castle Cliff, Washington Co., *Eastwood & Howell No. 9052* (CAS); St. George, Washington Co., *Jones No. 1610* (CAS, CM, NY, P,RM, UA, UC, US, WS); near east entrance to Zion National Park, Kane Co., *Maguire No. 21313* (CAS, UC).

ARIZONA: Yucca, Mohave Co., *Jones No. 3912* (CAS, CM, DS, P, RM, UA, UC, US); foothills east of Hualpi Mt., Mohave Co., *Kearney & Peebles No. 11269* (CAS, NY, P, S, US); Yampai Valley, Yavapai Co., *Newberry in 1858* (NY, US); Skull Valley, Yavapai Co., *Jones in 1903* (P); Wickenburg, Valley of Hassayampa, Maricopa Co., *Palmer No. 623* (CM, G, M, NY, UC, US).

Phacelia Fremontii is the most abundant species in sect. *Euglypta* and it is perhaps also the most variable. Plants occur in many different situations and vary from erect individuals with solitary slender stems to robust plants with numerous spreading stems. Not only do the leaves vary in size, shape, and lobing, but the flowers vary from relatively small to quite large, the flowers with larger corollas being among the most attractive in the genus. Although there is so much variation in the species, none of the forms is here recognized taxonomically since it is practically impossible to delimit the variants.

Undoubtedly it was Brand's intention to segregate the smaller-flowered form of *P. Fremontii* as *P. Hallii* but the limits between the two variants if they are spearated would have to be highly arbitrary and the entities would have little distributional significance. Although I believe that the larger or smaller corollas of certain forms may result from genetic differences, the usefulness of flower-size as a taxonomic criterion is practically nullified by variations which may be due not only to climatic factors but even to the age of the plant. Thus flower-size may vary considerably in a locality from year to year depending on the amount of rainfall; and even on the same plant later flowers are usually much smaller than early ones. I believe that Jepson (1943, p. 279) is quite right in treating *P. Hallii* as a synonym of *P. Fremontii* and I am following the same course.

Jepson (1943, p. 280) has also treated *P. bicolor* Torr. as a synonym of *P. Fremontii* and, because I have had some difficulty in separating the two as species, I have prepared a table setting forth a number of characters in which they are notably divergent. Although it is true that in the case of most of these characters there are confusing intermediates which bridge the differences, the examination of several hundred collections has shown that nearly all the

intermediates occur in the Mohave Desert and Owens Valley of California where the ranges of the two species overlap. Thus in Owens Valley the habit of *P. bicolor* is more like that of *P. Fremontii* and along the southern Mohave border in the San Bernardino Mts. *P. Fremontii* looks like *P. bicolor*. In the Mohave Desert there is sometimes a reversal in the shapes of the corollas of the two species, and in the same region the filaments of *P. bicolor* are always glabrous, while those of *P. Fremontii* are occasionally pubescent. The extent to which the corolla-scales are attached to the filaments is almost finally dignostic of the two, although in the Mohavan area an occasional plant of *P. Fremontii* will exhibit a tendency towards *P. bicolor* even in this critical character.

Although the plants corresponding to the historical types of *P. bicolor* and *P. Fremontii* are distinct enough to be accepted generally as representing two species, I believe that the proper acceptance of these entities depends on how we interpret the occasional intermediate plants which are found in the Mohavan region of California. If we believe that these intermediates are the direct descendants and present day representatives of the complex from which the two entities originated, then we must accept these entities as two morphologically divergent branches which are not sufficiently separated from the original complex to be accorded more than subspecific recognition. In this view, the Mohavan area would be interpreted as the place of origin and center of dispersal of the *Fremontii-bicolor* complex. If, however, we believe that the Mohavan intermediates are the result of hybridization between two entities which have originated independently of each other, then I believe that the two entities should be accepted as distinct species. This latter view would imply that one or the other of the entities originated elsewhere than in the Mohavan area and that due to plant migrations in relatively recent times they have come to occupy in common a relatively small part of their respective ranges.

I believe that considerations from both the morphology and geographic distribution of these two entities support the latter view. Beyond the Owens Valley and the western part of the Mohave Desert, each of these entities may be differentiated by a series of distinctive and constant characters, the most important of which are listed in the accompanying table. Outstanding among these characters are the distinctive habits which not only furnish a ready and convenient way for distinguishing the two plants, but perhaps indicate the real relationships of the two species. The leafy habit of *P. bicolor* at once recalls the habit of *P. Leibergii* and of *P. glandulifera* and the less leafy stems of *P. Fremontii* are distinctly reminiscent of the subscapose stems of *P. affinis*. Certainly as far as geographic distribution is concerned, *P. bicolor* is typically developed and most common on the sagebrush lands of the western Great Basin and it undoubtedly represents a part of the specific segregations in that complex from which have been derived the other Basin and Columbian species, *P. Leibergii* and *P. glandulifera*. *Phacelia Fremontii* on the other hand, is typically an inhabitant of the higher plains and slopes along the northern borders of the Sonoran desert where the creosote-bush abounds, and it seems

probable that it and *P. brachyloba* may be more closely related to the wide-ranging *P. affinis* than to any other species. As I interpret the distribution of the several entities and their probable relationship, I would judge that neither *P. Fremontii* nor *P. bicolor* originated in that part of the Mohave Desert where present-day intermediates between them are occasionally found, but, that due to a southward dispersal of *P. bicolor* and a northwestward dispersal of *P. Fremontii* the two species have come to occupy a common area. That *P. Fremontii* has found the Mohave Desert a most agreeable home may be inferred by the overwhelming abundance and relative luxuriance of its individuals as compared to those of *P. bicolor* which has apparently not been benefited by its altitudinal and latitudinal descent from the Basin.

According to both Mary K. Curran (1885, p. 142) and Asa Gray (1886, p. 418), *P. Brannani* Kell. is to be referred to synonymy under *P. Fremontii*. In the absence of the type-specimen or any further critical data, the name is left here, since there is nothing in the original description to indicate that the plant described belonged to any other species in this section. Jepson (1943) apparently does not list *P. Brannani*.

Table Contrasting the Characters of *P. Fremontii* and *P. bicolor*

	P. Fremontii	*P. bicolor*
Habit	Inflorescence generally well projected above leafy part of plant	Inflorescence not generally projected above leafy part of plant
Pubescence of leaves	Frequently subappressed on upper surface of blade	Hirsutulous - spreading on upper surface and margin of blade
Calyx-segments	Tending to be oblanceolate-spatulate	Mostly narrowly oblanceolate and scarcely spatulate
Corolla	Generally salverform-funnelform with showy spreading limb	Mostly tubular - funnelform with narrower less spreading limb
Corolla-scales	Usually conspicuous and attached to filaments near base, the free part more than half the length of entire scale, the broadest part usually well above point of attachment to filament	Usually inconspicuous and attached to filaments through most of length, the broadest part of scale at point of attachment or just above
Anthers	Generally 0.75-1 mm. long	Generally 0.5-0.75 mm. long
Filaments	Glabrous (except occasionally in the Mohave Desert), markedly flattened below middle	Hairy (except in Mohave Desert and just to the north), mostly round, rarely flattened
Seeds	Corrugations rather coarse and mostly 6-8, very rarely to 10	Corrugations finer and mostly 8-10, rarely to 11 or 12

4. PHACELIA BRACHYLOBA (Benth.) Gray Proc. Amer. Acad. **10**:324 (1875)

Eutoca brachyloba Benth., Trans. Linn. Soc. **17**:277 (1835).
P. Cooperae Gray, Proc. Amer. Acad. **15**:49 (1879)
P. Orcuttiana Gray, Proc. Amer. Acad. **19**:88 (1883).
P. leucantha Lemmon ex Greene, Pittonia **1**:175 (1888).

Root annual; stems substrictly erect, simple below and corymbosely few-branched above, or widely branched from the base, the branches ascending, 1-7 dm. tall, usually about 3 dm. tall, hirsutulous and capitate-glandular, the glands very numerous in the upper part of the plant, equaling or a little longer than the nonglandular hairs; leaves 1-3.5 cm. long, 0.3-1.5 cm. wide, or in vigorous plants as much as 15 cm. long and 5 cm. wide, oblanceolate to narrowly elliptical, mostly near the base but usually not rosulately congested, stems leafy up to the inflorescence but cauline leaves sparsely scattered, the uppermost much reduced, pinnately divided and somewhat lyrate, the divisions oblong or oblong-ovate, obtuse, entire or lobed, the uppermost leaves sometimes only crenate-lobed or rarely even subentire, subappressed-hirsutulous above, hirsutulous and more or less glandular below, petioles elongate below, to 3 (or 8) cm. long, much shorter above; racemes corymbosely arranged at the top of the stem and conspicuously exceeding the leafy part of the plant, becoming markedly elongate and to 2.5 dm. long, the flowers evenly and approximately disposed (or the lowest a little separated) on pedicels 1-4 mm. long; calyx-segments in flower 4-5 mm. long, 0.6-1 mm. wide, linear-oblanceolate, in fruit a little accrescent, 5-6.5 mm. long, 0.75-2 mm. wide, linear-oblanceolate to broadly oblanceolate, obtuse, glandular and hirsutulous; corolla funnelform-salverform to campanulate, 7-10 mm. long, to 15 mm. wide, limb white to pink, subrotately but not horizontally spreading, lobes 2-3 mm. long, the lobes and throat minutely papillate inside, the tube areolate-venulose, yellow with deep yellow veins; corolla-scales narrowly semi-linear-elliptic, attenuate above and below, 2-3 mm. long, free from the filaments, or scales obsolescent or none; stamens unequal to nearly equal in length, 4-5 mm. long, anthers 0.75-1 mm. long, oblong, filaments glabrous, broad, attached a little above the base of corolla, filaments at base outwardly bowed, the corolla a little concave inward below point of attachment of filaments; style and branches 3-4 mm. long, branches 0.5-1 mm. long, style hairy to the middle or above; ovary 1-1.3 mm. long, the hypogynous disk thick and conspicuous, ovules "about 8" (acc. Gray) or 20-53; capsule oblong, rounded to truncately obtuse, prominently apiculate, 4-5 mm. long, 2-2.5 mm. wide, longitudinally sulcate on the back, hirsutulous above, puberulent or glabrous below, very sparsely glandular; seeds 0.6-1 mm. long, plumply ovate or elliptic-ovate, brownish, finely but definitely transversely corrugated and rather coarsely longitudinally lineate, the seed in certain light appearing only coarsely foveolate, corrugations 5-7, thick and rounded.

Gravelly or sandy soil of mountain slopes and flats, occurring abundantly and characteristically in areas of chaparrel following fire, from Monterey and San Benito counties, California, southward to the mountains of northern Lower California.

Representative collections: CALIFORNIA: California, *Douglas* (G, type-collection); Del Monte Heights, Seaside, Monterey Co., *Loveday in 1912* (CAS); Carmel, Monterey Co., *Rowntree in 1928* (CAS); canyon of Arroyo Seco River, Santa Lucia Mts., Monterey Co., *Eastwood & Howell No. 2417* (CAS); Pinnacles, San Benito Co., *J. T. Howell No. 12929* (CAS); Atascadero, San Luis Obispo Co., *Seitz in 1927* (CAS); Painted Cave Ranch, Santa Barbara Co., *Eastwood No. 72* (CAS, CM, G, M, NY, UC, US); Santa Barbara, Santa Barbara Co., *Mrs. Elwood Cooper in 1879* (G, type of *P. Cooperae*), *Torrey No. 350* (G, NY, US); upper Sespe Creek, Ventura Co., *Chester Dudley in 1939* (CAS); Ojai Valley, Ventura Co., *Hubby in 1896* (G, UC), *Fauntleroy in 1918* (CAS); Ridge Route near summit, Los Angeles Co., *Epling & Wheeler No. 1758* (CAS, DS, M, UC); Mint Canyon, Los Angeles Co., *Ripley & Barneby No. 5195* (CAS, RB); divide between Fish and Monrovia canyons, San Gabriel Mts., Los Angeles Co., *J. T. Howell No. 3885* (CAS, DS); southern slope of San Bernardino Mts., San Bernardino Co., *Parish No. 7074* (CAS, CM, DS, G, M, NY, P, RM, UA, UC); Colton, Riverside Co., *Jones in 1882* (DS, G, P); near Idyllwild, San Jacinto Mts., Riverside Co., *J. T. Howell No. 2918* (CAS, RSA); Santiago Peak, Santa Ana Mts., Riverside Co., *J. T. Howell No. 6612* (CAS, M, US, WS); 10 miles north of Warners Hot Springs, San Diego Co., *J. T. Howell No. 4818* (CAS, CM, G, UN); Jacumba, San Diego Co., *Eastwood No. 9557* (CAS), *Jones in 1926* (CAS, DS, UC); Del Mar, San Diego Co., *Angier in 1894* (topotype of *P. leucantha;* DS, G, M, UA, UC).

LOWER CALIFORNIA: Mountains near Campo, *Orcutt No. 838* (G, type of *P. Orcuttiana;* UC); Nachoguero Valley, *Schoenfeldt No. 3407* (DS, US); Vallecitos, Sierra San Pedro Martir, *Wiggins & Demaree No. 5049* (CM, DS, NY, P, UC, US).

It would appear that Asa Gray never realized that *P. brachyloba* belonged to sect. *Euglypta,* and, undoubtedly because of this misunderstanding, he described *P. Orcuttiana,* an entity scarcely representing a Grayian species as distinct from *P. brachyloba.* Although Parish (1898, p. 90) was the first to report that *P. Orcuttiana* and *P. leucantha* Lemmon belonged to *P. brachyloba,* it was not until Brand published his monograph in 1913 that *P. Cooperae* Gray was transferred as a synonym to *P. brachyloba* from *P. gymnoclada* where Gray had referred it in 1886 (p. 418).

On the basis of somewhat variable technical characters that are more or less correlated with the distribution of the species, several variants might be distinguished taxonomically, but, since they are not especially marked in appearance and tend to intergrade, they will be indicated here but not named. The typical form of *P. brachyloba,* which occurs in Monterey County at the northern distributional limit of the species, has corollas with white limb and corolla-scales quite evident. Just to the south in Santa Barbara and Ventura counties occurs the form corresponding to *P. Cooperae* Gray and in this the corolla-tube is more cylindric-elongate, the corolla-limb is pink, and the stamens tend to be unequal in length. It is in well-developed plants of this form that *P. brachyloba* approaches *P. Fremontii* most closely, in some instances retaining only the distinctive seed-character of *P. brachyloba* which seems to be entirely reliable. In the mountains of southern California and northern Lower California the corolla-tube is more campanulate just as is the typical form to the northward in Monterey County, but in the south the corolla-scales are lacking and the color of the corolla-limb varies from white to pink, sometimes in the same area. It was this plant from southern California and Lower California that received the names *P. Orcuttiana* and *P. leucantha.* Finally in the

mountains of Lower California at the southern distributional limit of the species a form has been collected in which the uppermost leaves are frequently subentire. Since numerous intergrades break down the apparent distinctions between these different forms, it has seemed best to treat them as parts of a single variable species without named varieties.

5. PHACELIA GYMNOCLADA Torr. ex Wats. Bot. U. S. Geol. Explor. 40th Paral. (King's Exped.) 255 (1871)

P. crassifolia Torr. ex Wats., l. c.

Root annual; stems branching from the base, the principal branches usually several, spreading and ascending, mostly 0.5-2 dm. long, the lower internodes markedly elongate, hirsutulous with spreading and reflexed hairs, glandular hairs sometimes almost lacking, generally more numerous on the upper branches and in the inflorescence; basal leaves few in a loose rosette, the cauline frequently opposite or subopposite, rather numerous and well developed, elliptical to ovate or rarely almost round, pinnately lobed or pinnately serrate to crenate-serrate or entire, mostly 1-2.5 or 3 cm. long, 0.3-1.5 cm. wide, hirsutulous, the hairs subappressed above, apex obtuse or acute, at base narrowly to broadly cuneate or rarely rounded, petioles to 3 cm. long, the lowest usually equaling or longer than the blades, much shorter and sometimes nearly lacking above; racemes elongate but not conspicuously raised above the leafy parts of the plant, more or less leafy-bracteate, to 12 cm. long, generally sessile, flowers distant below, crowded above, pedicels mostly 1-5 (or even 9) mm. long, those of lowest flowers reflexed or sigmoid-spreading; calyx-divisions in flower 3-5 mm. long, in fruit 5-8 mm. long, 0.5-1 mm. wide, linear to linear-oblanceolate, the tips straight or spreading a little, rarely a little spatulate, hirsutulous and more or less glandular or sometimes not at all glandular; corolla campanulate-funnelform, 6-10 mm. long and about as broad, the limb spreading, blue to lavender, the lobes 1.5-2 mm. long, the tube yellow; corolla-scales semi-linear-lanceolate, 1.5-3 mm. long, attenuate above into a fine line, below attached to the base of the filaments and forming a shallow pocket; stamens attached about 0.5 mm. above base of corolla, unequal, 3-5 mm. long, anthers 0.5-0.66 mm. long, filament hairy below the middle; style and branches 2.5-4 mm. long, the branches 0.5-1 mm. long, the style bristly-hairy to about the middle; ovary about 1 mm. long, ovules 8-14; capsule oblongish or tending to be a little wider above the middle, 3-4 mm. long, 2-2.5 mm. wide, obtuse, very shortly apiculate, thinly pilose, the back of the valves longitudinally sulcate; seeds narrowly to plumply ovate or oblongish, 1-1.75 mm. long, corrugations mostly rounded, 7-9.

A rather widely distributed but uncommon plant occurring on dry gravelly slopes or alkaline flats from southeastern Oregon southward to middle western Nevada and adjacent California. A vivid account of the field occurrence of *P. gymnoclada* at the type-locality of *P. glaberrima* (Torr.) J. T. Howell and in the type-region of *P. crassifolia* has been given by R. C. Barneby (1944, p. 368).

Representative collections: OREGON, all in Harney County: Lower Willow Creek Canyon, *Peck No. 18993* (W); 7 miles south of French Glen, *Peck No. 18960* (W); between Fields and Andrews, *Applegate No. 5609* (DS, W); Pueblo Mts., *Henderson No. 8705* (CAS).

NEVADA: Trinity Mts., Pershing Co., *Watson No. 881* in part (type, NY); Unionville Valley, Pershing Co., *Watson No. 881* in part (US); Truckee Pass, Washoe Co., *Watson No. 881* in part (G); Reese River Valley, Lander Co., *Watson No. 882* (G, type-collection of *P. crassifolia*); Reese River Valley, 26 miles south of Battle Mt., Lander Co., *Ripley & Barneby No. 6172* (CAS); near Rochester, Pershing Co., *Train* (US); 10 miles east of Reno, Washoe Co., *Lehenbauer No. 2693* (UN, flowers white); Pyramid Lake, Washoe Co., *Frandsen & Brown No. 343* (UN); Petrified Forest, Wilson Canyon, Lyon Co., *Lehenbauer No. 169* (UN); west of Eastgate, Churchill Co., *Ripley & Barneby No. 5937* (CAS); Springer's Hot Springs, Churchill Co., *Ripley & Barneby No. 5651* (CAS); Lahontan, Churchill Co., *Headley No. 9* (US); Hawthorne, Mineral Co., *Jones No. 3983* (CAS, CM, M, NY, P, US); Montgomery Pass, Mineral Co., *Ripley & Barneby No. 3709* (CAS), *Eastwood & Howell No. 9537* (CAS); 1 mile northwest of Tonopah, Nye Co., *Ripley & Barneby No. 3674* (CAS, RM); 7 miles north of Arlemont, Esmeralda Co., *Linsdale in 1927* (CAS); Pinchot Creek, White Mts., Esmeralda Co., *Duran No. 3261* (CAS, CM, DS, G, M, NY, P, RM, RSA, UC, WS).

CALIFORNIA: "Sierra Nevada Mts.," probably in Sierra Co., *Lemmon in 1875* (CAS, US); Mono Lake, Mono Co. (acc. Brand, 1913, p. 129); summit, Owens Valley, 7000 ft., Inyo or Mono Co., *Jones in 1897* (M, P, US).

Phacelia gymnoclada presents a rather diverse appearance over its range but the fact that almost equally divergent forms have been seen and collected from a relatively restricted area between the White Mountains and Tonopah in Nevada leads me to interpret the variations as chiefly edaphic in character. In southern Oregon a markedly glandular variant with shorter lower internodes is found but since similar forms found in Nevada seem to intergrade with more typical aspects of the species, it is not recognized at present. Certainly further data on the occurrence and stability of variations in this species seem necessary before varieties may be adequately delimited.

Through the cooperation of the Gray Herbarium and the New York Botanical Garden I have been able to examine specimens from the original collections of both *P. gymnoclada* and *P. crassifolia*. The type plant of *P. gymnoclada*, which in aspect is quite like most of the specimens from Nevada, is very young, since it was collected at 5000 feet in May. *Phacelia crassifolia* as represented in the Gray Herbarium consists of a single branch which bears the cymose-paniculate arrangement of racemes and branchlets that is characteristic of this relationship. Comparing these critical collections of *P. gymnoclada* and *P. crassifolia*, the pubescence of the latter is more glandular, the uppermost leaves reduced and entire, the racemes more compact, the flower-parts smaller, and the capsules smaller and sometimes abortive. I cannot see in any of these differences a character of specific value, particularly since the collection of *P. crassifolia* represents a fully matured and late-fruiting plant collected in July. Hence, until we have further collections on which a fair estimate of *P. crassifolia* may be based, I shall treat it as merely a senile phase of *P. gymnoclada*.

The relationship of *P. gymnoclada* is not obvious. It is perhaps most closely related to *P. bicolor* and *P. Fremontii*, both of which it closely resembles

in characters of the flowers and fruit. However, in the rather outstanding tendencies for the racemes to be sessile, for the lowest pedicels in the racemes to become reflexed in fruit, and for the capsule to be a little widened upward, *P. gymnoclada* differs from the *P. Fremontii* type and resembles *P. Ivesiana.* Although the corollas of *P. gymnoclada* are always larger and showier than in *P. Ivesiana,* there is to be noted in the latter a definite tendency for the rhachis of the leaves to become broadened which is one of the most obvious differences between *P. gymnoclada* and *P. Fremontii.* On the other hand I am not inclined to ally *P. gymnoclada* to *P. pachyphylla* Gray and its relatives as closely as may be inferred from the keys by Brand (1913, p. 125) or Jepson (1943, p. 244). Although the lowest flowers in the frequently sessile racemes of *P. pachyphylla* and *P. neglecta* M. E. Jones are often pendent, there is nothing in the habit, foliage or flowers of *P. gymnoclada* to emphasize a close connection; and the turgidly subglobose capsules that frequently exceed the fruiting calyx in *P. pachyphylla, P. calthifolia,* and *P. neglecta* is a character entirely divergent from all other species in the section except as it is suggested as an occasional tendency in the undoubtedly primitive *P. Ivesiana* complex. At present I prefer to think of *P. gymnoclada* as a northward extension of the *P. Fremontii* complex, but yet an entity strongly reminiscent of *P. Ivesiana.*

6. PHACELIA IVESIANA Torr., in Ives' Colo. River Explor. Exped. Bot. 21 (1860)

Stems several to many from a rather stout annual taproot, erect or widely spreading, mostly 0.5-2.5 dm. long, sparsely to rather densely hirsutulous and very finely and generally densely viscidulous-puberulent, the nonglandular hairs divaricate and much longer than the glandular hairs, the glandular hairs only rarely lengthening and capitate in the inflorescence, the glands never black; leaves rather scattered, the basal leaves few, blades oblongish to oblanceolate, 1-3.5 cm. long, 0.5-1.2 cm. wide, pinnately divided or sometimes only deeply lobed, the segments narrowly oblong to broadly deltoid, entire or rarely toothed, hirsutulous and generally a little glandular beneath, petioles to 4 cm. long; racemes usually not exceeding the leafy part of the plant, sessile, the lower flowers distant, the upper approximate but not congested, pedicels 2-6 mm. long below, the uppermost much shorter and only 0.5-1 mm. long, the lowest frequently becoming reflexed or sigmoid-spreading in fruit; calyx-segments in flower 2.5-4 mm. long and 0.5-0.75 mm. wide, in fruit somewhat accrescent and becoming 5-7 mm. long, 0.5-1.25 mm. wide, narrowly oblong to oblong-oblanceolate, usually not spatulate, the tips spreading, sparsely hirsute and viscidulous-pubescent, the base of the calyx frequently cupulate and more or less angled by thickened protruding veins; corolla tubular-funnelform, 2.5-4 mm. long, the limb white, 0.75-1 mm. long, the tube yellowish; corolla-scales small or obsolete, filiform to semi-linear-lanceolate, 0.5-1 mm. long, free from the filaments; stamens attached above the base of the corolla, about equal, 1.25-2 mm. long, filaments glabrous, anthers about 0.2 mm. long, roundish or broader than long; style and branches 0.75-1.5 mm. (or rarely to 1.75 mm.) long, the branches 0.25-0.5 mm. long, style nearly glabrous or more or less hairy; ovary 1 mm. long, sparsely hirsutulous, ovules 11-20; capsule generally

oblong or elliptic, sometimes tending to be obovate, obtuse to truncate, 3.5-4.5 mm. long, 2-2.5 mm. wide, sulcate, puberulent with scattered hispidulous hairs near the top; seeds oblong-lanceolate to ovate, 1-1.5 mm. long, both ends acute, or one obtuse to subtruncate, brown, corrugations subobtuse or acute, 5-10 (or 12).

Two distinctive variants are discernible in *P. Ivesiana* and they can be rather easily distinguished by the shape and corrugations of the seeds. The most widespread form, the distribution of which centers in southern Utah, has narrowly oblong-oblanceolate seeds in which the corrugations number 8 to 12. The second form, restricted to the lower desert valleys of California, Nevada, and Arizona, has ovate or more plumply oblong seeds in which the corrugations number 5 to 7. The seed-characters of these two forms are correlated with foliage-characters which are frequently almost as marked, and, although the difference in the leaves become somewhat obscure in older plants, they give to the plants rather distinctive aspects.

Since the distribution of these variants overlap in eastern California, southern Nevada, and western Arizona, the problem of establishing the identity of var. *typica* has been a critical one, especially since the original description does not furnish a sufficiently detailed account of the seeds and since the several collections cited in the original description probably included specimens of both forms. The localities cited extended from north central Arizona on the east to the lower part of the Colorado River below the present site of Boulder Dam on the west and were designated as follows: "Diamond river; April 3. Sandy hills, Oraybe; May 13. Banks of the Colorado, March 20. Camp 49. . ." An examination of the type, which was loaned to me from Herb. Torrey. by the New York Botanical Garden, disclosed that the two kinds of plants are on the type sheet but there is no indication where they originated, the only data being "Ives' Colorado Expedn. *Dr. Newberry.*" Two of the three specimens represent the widespread upland form of the species while the third specimen is characteristic of the more depauperate phase of the lowland form. I am accepting the specimens of the former variant as typifying the species.

KEY TO THE VARIETIES OF PHACELIA IVESIANA

Seeds narrowly oblong to oblong-lanceolate, acute, corrugations 8-12 .....6a. var. *typica*
Seeds plumply oblong to ovate, obtuse or truncate at base, corrugations 5-7 .....
.....6b. var. *pediculoides*

6a. **Phacelia Ivesiana** Torr. var. **typica**, nom. nov.

Phacelia Ivesiana Torr., l. c.
P. campestris A. Nels., Bull. Torr. Bot. Club **26**:242 (1899).
P. Ivesiana Torr. f. *campestris* (A. Nels.) Brand. Das Pflanzenr. IV. **251**:126 (1913).
Miltitzia pinnatifida Osterhout, Bull. Torr. Bot. Club **53**:35 (1926).

Leaves usually divided nearly to the midrib, the segments mostly narrowly oblong, petioles shorter than the blades or a little longer; calyx-segments of lower flowers generally divided nearly to the base of calyx; style and branches 0.75-1 mm. long; capsule oblong to elliptic-oblong, usually not widened above;

seeds narrowly oblong to oblong-lanceolate, acute at both ends, corrugations 8 to 10 or even 12.

Sandy soil of sagebrush plains, mountain slopes, and dunes from southern Wyoming and western Colorado south to western New Mexico and Arizona and west to southern Nevada and southeastern California.

Representative collections: WYOMING: Fort Steele, Carbon Co., *Tweedy No. 4566* (NY, US); Granger, Sweetwater Co., *A. Nelson No. 4696a* (RM, type of *P. campestris*); 21 miles west of Green River, Sweetwater Co., *Payson & Armstrong No. 3208* (G, M, RM).

UTAH: Vicinity of Flaming Gorge, Daggett Co., *L. Williams No. 475* (CAS, G, M, RM); between Vernal and Lapoint, Uintah Co., *Graham No. 8803* (CAS, US); Stansbury Island, Tooele Co., *Watson in 1869* (G, NY, US); Simpson's Springs, Juab Co., *Cottam No. 7631* (UU); Deseret, Millard Co., *Jones in 1880* (P); Milford, Beaver Co., *Stokes in 1903* (US); Belknap, Sevier Co., *Stokes in 1900* (DS, NY, US); Emery, Emery Co., *Jones No. 5449* (CAS, M, NY, P, UC, US); Moab, Grand Co., *Jones in 1913* (P); 7 miles east-southeast of Teasdale, Wayne Co., *Harrison No. 7533* (M); Bluff, San Juan Co., *Jones in 1919* (P); 8 miles north of Kanab, Kane Co., *Eastwood & Howell No. 9274* (CAS); between Leeds and Oak Grove, Washington Co., *Eastwood & Howell 9166* (CAS, UU, W); St. George, Washington Co., *Jones No. 1626* (CAS, CM, DS, NY, P, RM, UA, US, UU).

COLORADO: West of Craig, Moffat Co., *Osterhout No. 6393* (RM, type of *Miltitzia pinnatifida*; G, M); Grand Junction, Mesa Co., *Eastwood No. 5108* (CAS), *Macbride No. 700* (G, RM).

NEW MEXICO: Ojo Caliente, about 13 miles southwest of Zuni Pueblo, McKinley Co., *Hodge in 1919* (US).

IDAHO: Thirteen miles west of Glenns Ferry, Elmore Co., *Davis No. 1939* in part (UI); Bruneau, Owyhee Co., *Ripley & Barneby No. 6498* ("a single individual seen;" CAS).

NEVADA: Currie, Elko Co., *Jones in 1906* (P); Ely, White Pine Co., *Ripley & Barneby No. 3641* in part (RB); foothills of Lone Mt. west of Eureka, Eureka Co., *Ripley & Barneby in 1944* (CAS); foothills of Needle Mts. east of Peck Station, Lincoln Co., *Ripley & Barneby No. 6415* (CAS); south of Red Rocks, Charleston Mts., Clark Co., *Clokey No. 8724* (CAS, M, NY, P, UA, WS); southwest of Crystal, Clark Co., *Eastwood & Howell No. 9005* (CAS); Moapa, Clark Co., *Kennedy No. 1814* (CAS, CM, DS, NY, US).

ARIZONA: Ives' Colorado Expedition, *Newberry* (NY, type); near Rock Point, Apache Co., *Peebles & Smith No. 13524* (CAS, S); Oraibe, Navajo Co., *Newberry in 1858* (US); Shonto to Betatakin, Navajo Co., *Peebles & Fulton No. 11900* (CM, G, NY, S, US); 8 miles above Pierce's Ferry, Mohave Co., *Jones No. 5077a* (P, US); Mesquite to Littlefield, Mohave Co., *Kearney & Peebles No. 13183* (S).

CALIFORNIA: Kelso, San Bernardino Co., *K. Brandegee in 1915* (UC); 7 miles south of Kelso, San Bernardino Co., *Wolf No. 10197* (RSA).

A detailed account of the distribution of *P. Ivesiana* is given under *P. glandulifera*, where the distinctive ranges of the two species are contrasted. Only four collections have been seen which indicate the overlapping in distribution of the two species: in southern Idaho, where specimens of *P. Ivesiana* have been collected by Prof. R. J. Davis and by Ripley and Barneby in the Columbia-Snake River drainage, and in southwestern Wyoming, where two specimens of *P. glandulifera* have been collected by Prof. A. Nelson in the Colorado-Green River drainage. Prof. Davis' collection from southern Idaho

is further noteworthy in that it consists of plants of both species which Prof. Davis assures me grew "side by side and very close to each other."

Attention should be called to Sereno Watson's collections made on the King Expedition which were listed as *P. Ivesiana* in the botany of the expedition under number 879 (Bot. King's Exped., p. 254). Three species are involved: *P. Ivesiana* from Stansbury Island; *P. affinis* from the Coyote Mts. and east Humboldt Mts.; and *P. glandulifera* from Monitor Valley. Of the two other collections cited, the Ives collection is presumably *P. Ivesiana*, while Palmer's collection from southern Utah in 1870 (*Palmer No. 3*) is *P. affinis*.

A minor variant of var. *typica* which has a rather definite geographic range occurs west of the Rocky Mts. between southwestern Wyoming and northern Arizona. In this form the glands of the inflorescence have elongate shining stalks as in *P. affinis* and *P. glandulifera* and the habit is somewhat more robust. Because these characters occur sporadically (though rarely) throughout the range of the species, the variant should probably not be named, but some of the specimens with these characters may be cited here:

WYOMING: Twenty-five miles south of Green River, Sweetwater Co., *Maguire et al. No. 12369* (UC).

UTAH: Twelve miles south of Manila, Daggett Co., *Hitchcock et al. No. 3912* (CAS, DS, RM, UW, WS); Green River, Emery Co., *Jones in 1890* (P).

COLORADO: Grand Junction, Mesa Co., *Jones in 1895* (P).

ARIZONA: Navajo Spring, Coconino Co., *Jones in 1890* (P).

6b. **Phacelia Ivesiana** Torr. var. **pediculoides**, var. nov.

A var. *typica* differt: foliis saepe tantum partitis vel lobatis et segmentis deltoideis, petiolis laminis plerumque longioribus; calyce inferiore in fructu basi saepe cupulato et subangulato; stylo et ramis 1-1.75 mm. longis; capsulis oblongis vel inferioribus conspicue latiusculis apice et subobovatis; seminibus pediculoideis, turgide oblongis ovatisve, obtusis vel truncatis basi, rugis plerumque 5 vel 7.

Type: Herb. Calif. Acad. Sci. No. 253726, collected on dunes at Lost City near Overton, Clark Co., Nevada, *Munz & Youngberg No. 14903*, April 5, 1937. Isotypes: FP, M, P, RM, UC.

Other collections: NEVADA: Amargosa Desert, Nye Co., *Jones in 1907* (DS, P); Vegas Wash, Clark Co., *Coville & Funston No. 421* (US).

CALIFORNIA: Panamint Valley, Inyo Co., *Coville & Funston No. 684* (CAS, CM, DS, G, M, NY, US); Yucca (now Muroc), Kern Co., *K. Brandegee in 1884* (UC); Twenty-nine Palms, San Bernardino Co., *T. S. Brandegee in 1902* (UC); Needles, San Bernardino Co., *Jones No. 3839* (CM, G, P, US); 15 miles southeast of Coachella, Riverside Co., *Peirson No. 2856* (FP, UC); Borego Spring, San Diego Co., *T. S. Brandegee in 1895* (UC); Chocolate Mts., Imperial Co., *Winblad in 1937* (CAS).

ARIZONA: Willow Beach, Mohave Co., *Clokey No. 5915* (in part var. *typica*?, CAS, NY, WS); Wellton, Yuma Co., *Kearney & Peebles No. 10916* (P, S, US); Wickenburg, Hassayampa Valley, Maricopa Co., *Palmer No. 622* (CM, G, M, NY, US).

7. PHACELIA GLANDULIFERA Piper Contrib. U. S. Nat. Herb. 11: 472 (1906)

P. luteopurpurea A. Nels., Bot. Gaz. **52**:271 (1911).
P. Ivesiana Torr. f. *glandulifera* (Piper) Brand, Das Pflanzenr. IV. **251**:126 (1913).
P. Ivesiana Torr. var. *glandulifera* (Piper) Nels. & Macbr., Contrib. Gray Herb. n. ser. **49**:40 (1917).

Plants annual, 0.3-3 dm. tall, few- to many-branched from the base or above, the branches fastigiately to substrictly erect or rarely more widely paniculate, strongly purplish-tinged, hirsutulous and capitate-glandular, the nonglandular hairs sometimes dense and retrorse at base of plant, the glandular hairs with shining and translucent stalks, the glands dark brown or black; leaves mostly scattered and not rosulate, irregularly bipinnatifid, the main divisions again deeply parted or divided and frequently alternating with the shorter entire intermediate lobes, the blades 2-4 cm. long, 1-2 cm. wide, hirsutulous above, hirsutulous and capitate-glandular below, petioles to 2.5 cm. long; racemes not conspicuously exceeding the leafy part of the plant, the lowest flowers distant, the uppermost approximate, lower pedicels 1-5 mm. long, almost none above; calyx-segments in flower 4-7 mm. long, 0.3-1 mm. wide, in fruit 5.3-10 (or even 15) mm. long, 0.5-1.5 mm. wide, linear to linear-oblanceolate, not spatulate, hirsutulous and capitate-glandular; corolla tubular-funnelform (4 or) 5-6.5 mm. long, the lobes lavender, the tube yellowish, 3.75-5 mm. long; corolla-scales 0.5-1 mm. long, semi-linear-lanceolate to semi-lanceolate-ovate, attached at base to filament and forming a conspicuous pocket; stamens unequal or nearly equal, 2-4 mm. long, attached well above base of corolla, the longer exserted from the corolla-throat, the filaments glabrous above, usually bearing a few hairs at point of attachment to scales, anthers 0.3 mm. long, roundish; style and branches 2-3 mm. long, the branches 0.2-0.5 mm. long, the style hairy to the middle; ovary about 1 mm. long, hirsutulous above, glabrous below, ovules 14-23; capsule elliptic-oblong, 4-5.5 mm. long, rounded-obtuse or acutish, hirsutulous above, puberulent below; seeds ovate, angular and somewhat twisted, obtuse at base, acute at apex, grayish-brown, corrugations 8-10, sharp and ribbed.

Loose or sandy soil of high plains or mountain slopes, from middle eastern California and central Nevada northward through eastern Oregon to eastern Washington, thence eastward through southern Idaho to southwestern Wyoming.

Representative collections: WYOMING: Point of Rocks, Sweetwater Co., *A. Nelson in 1898* (RM); Granger, Sweetwater Co., *A. Nelson No. 4696* (M).

IDAHO: Fremont Co., *Davis No. 364* (CAS, UC, UI); Terreton, Jefferson Co., *Davis No. 3817* (CAS, UC, UI); Picabo, Blaine Co., *Macbride & Payson No. 2980* (CAS, DS, G, M, NY, P, RM, UC, US); Raft River, Minidoka Co., *Davis No. 4-37* (UI); 10 miles south of Rogerson, Twin Falls Co., *Ripley & Barneby No. 6469* (CAS); King Hill, Elmore Co., *Nelson & Macbride No. 1141* (RM); 13 miles west of Glenns Ferry, Elmore Co., *Davis No. 1939* in part (UI); 11 miles south of Bruneau, Owyhee Co., *Davis in 1939* (CAS, UI); on tributary of Bruneau River, 8 miles southwest of Hot Spring, Owyhee Co., *Ripley & Barneby No. 6521* (CAS); New Plymouth, Payette Co., *Macbride No. 84* (RM, type of *P. luteopurpurea;* CAS, CM, DS, G, M, UC, WS).

WASHINGTON: Pasco, Franklin Co., *Piper No. 2954* (WS, type of *P. glandulifera;* G, P, US), *Henderson No. 2540* (UW); junction of Crab and Wilson creeks, Douglas Co., *Sandberg & Leiberg No. 306* (CAS, CM, G, M, NY, UC, US, WS).

OREGON: Sage plains, *Howell in 1885* (CAS, CM, DS, G, NY, US); 5 miles south of Redmond, Deschutes Co., *Peck No. 13813* (CM, DS, W); Ludlow, Crook Co., *Whited No. 3228* (US); Abert Lake, Lake Co., *Peck No. 20824* (CAS, W); canyon west of Adel, Lake Co., *Ripley & Barneby No. 6052* (CAS); Narrows, Harney Co., *Peck No. 6060, 6062* (W); Alvord Ranch, Steens Mts., Harney Co., *Henderson No. 8710* (CAS); 40 miles north of McDermitt, Malheur Co., *Peck No. 20603* (CAS, W); near Adrian, Malheur Co., *Henderson No. 8707* (CAS).

NEVADA: Cobre, Elko Co., *Ripley & Barneby No. 5520* (CAS); Wells, Elko Co., *Eastwood & Howell No. 307a* (CAS, CM); Monitor Valley, probably Eureka Co., *Watson in 1868* (G); Pinto Basin 10 miles south of Eureka, Eureka Co., *Train No. 292* (US); 12 miles north of Battle Mountain, Lander Co., *Holmgren No. 1068* (CAS); Toquima Range above Manhattan, Nye Co., *Ripley & Barneby No. 3669* (CAS); Cory Creek, Wassuk Range, Mineral Co., *Archer No. 6910* (UN); Chiatowich Creek, Esmeralda Co., *Duran in 1930* (CAS, CM, DS, G, M, NY, P, RM, RSA, UA, UC, US).

CALIFORNIA: Surprise Valley, Modoc Co., *Lemmon* (G, NY, UC); Devils Gate, Mono Co., *Ripley & Barneby No. 5811* (CAS).

Phacelia glandulifera, with its well-developed pocket behind the lower part of the filaments and the connivent corolla-scales, bears to *P. Ivesiana* somewhat the same relation *P. bicolor* bears to *P. Fremontii.* In each case the entities are separable only by critical characters which have not always been regarded as specific, although in both instances the characters are to be correlated with significant distributional patterns. In the case of *P. glandulifera* and *P. Ivesiana,* not only are the species separable by the staminal character mentioned, but the plants are very distinct in habit, they are usually clothed by different types of vestiture, the corollas are unlike in size and shape, the dimensions of the style are diagnostic, and the shape and sculpturing of the seeds are distinctive. I regard *P. glandulifera* as a very good species.

In only a single plant (part of *Davis No. 364*) have I found styles and branches 1.5 to 1.75 mm. long, and in only one specimen of *P. Ivesiana* (*M. E. Jones No. 3839*) have I measured style and branches as much as 1.75 mm. long. Of the numerous specimens of *P. Ivesiana* I have examined, only about a half dozen collections mostly from the Green River drainage exhibit the longer capitate glands resembling those of *P. glandulifera.* In these specimens besides the usual abbreviated glands characteristic of *P. Ivesiana,* there are abundant glands in the inflorescence borne on elongate translucent stalks, but it is perhaps noteworthy that the glandular secretion of both kinds of glands is light brown.

I believe that it is especially significant that the two species are characteristic of very different geographic provinces, *P. glandulifera* belonging chiefly to the Columbia River drainage and Great Basin, *P. Ivesiana* belonging to the Colorado River drainage. *Phacelia glandulifera* has not been collected southward in the Death Valley region in California or Nevada nor to the eastward in the Bonneville basin in Utah, the center of its distribution being in the northwestern part of the Great Basin in southeastern Oregon. *Phacelia Ivesiana,* on the other hand, has a remarkable range extending from the lower

Colorado River northward and eastward along its several principal tributaries into Wyoming, Colorado, and New Mexico. In eastern California, *P. Ivesiana* is found as far north as the Death Valley region, but this is historically a part of the Colorado drainage although it is now severed from it. In northwestern Utah, the distribution of *P. Ivesiana* extends beyond the Colorado drainage, there occupying, to the exclusion of *P. glandulifera*, the Bonneville basin which is historically a part of the Columbia drainage but at present a part of the Great Basin; and from southern Idaho along the Snake River, two collections of *P. Ivesiana* have been seen. In southwestern Wyoming, *P. glandulifera* has been twice collected in the drainage of the Green River, but no specimen of *P. glandulifera* has been seen from Utah and only a single specimen of *P. Ivesiana* is known from northeastern Nevada (Currie, Elko Co., *M. E. Jones in 1906*). Thus, out of more than a hundred collections that have been examined in these two species, only four have been seen which extend beyond the limits of the important physiographic regions which seem to bound them naturally, so it can be seen that the truly far-flung and remarkable ranges of the two are almost absolutely distinct.

I cannot see that there should be the vestige of a doubt concerning the specificity of these two entities, whose morphology is not only very distinct but whose origin and subsequent dispersal must have been related to, if not coincident with, the origin and development of several of the major geologic features of western America.

8. PHACELIA BICOLOR Torr. ex Wats. Bot. U. S. Geol. Explor. 40th Paral. (King's Exped.) 255 (1871)

Root annual; stems erect or spreading, 0.5-4.5 dm. long, simple below and branching above, or more commonly branching from the base, the branches usually markedly leafy and tending to branch and rebranch, hirsutulous and capitate-glandular; basal leaves few and clustered or scattered, the cauline usually well developed, ovate in outline, variously cleft, lobed, pinnately divided or characteristically coarsely to finely bipinnatisect, the segments oblong, ovate or roundish, obtuse, hirsutulous and more or less glandular, varying from cinereous and scarcely glandular to heavily glandular, 1-5 cm. long, 0.3-2.5 cm. wide, petioles to 5 cm. long, about equaling the blades; racemes not projected above the leafy part of the plant, peduncled, becoming elongate and to 1.5 dm. long, the flowers scattered below, approximate above, pedicels 1-4 mm. long; calyx-segments in flower linear to linear-oblanceolate, 2.5-6 mm. long, 0.3-1 mm. wide, in fruit 4-10 mm. long and 0.5-1.5 mm. wide, linear to linear-oblong or linear-oblanceolate, variously hirsutulous and capitate-glandular; corolla tubular-funnelform to campanulate-funnelform, 9-16 mm. long, to 1 cm. across, the limb from bluish-lavender to purplish or reddish-violet, the tube yellow and frequently prominently nerved, the lobes 2-2.5 mm. long, finely papillate inside, the tube finely glandular-puberulent outside; corolla-scales united below to the lower part of the filaments and forming with them a deep narrow pocket, the scales abruptly narrowed and linear-attenuate above the point of attachment to the filaments, the scales attached to filaments 1.5-3

mm., the upper free part of the scale about 1 mm. long; stamens unequal and frequently in two or three lengths, shorter than the corolla-tube, 4-7.5 mm. long, the filaments sparsely hairy near point of attachment with corolla-scales or rarely glabrous, anthers about 0.5-0.8 mm. long; style and branches 3-6 mm. long, the branches 0.5-1 mm. long, the style hairy and sometimes glandular to about the middle or a little above; ovary 1 mm. long, hirsutulous above, ovules 13-23; capsule rounded to elliptic-oblong, 4-6 mm. long, 2-2.5 mm. wide, obtuse and scarcely apiculate, sparsely hirsutulous and glandular especially above, sulcate on back of valves, the style tardily deciduous; seeds brown, ovatish with one end acute, back rounded, the front carinate-angled, 1-1.5 mm. long, corrugations 8-10, either sharp or rounded.

Sandy soil and dunes of desert valleys and mountains east of the Sierran crest from southern California and western Nevada northward to southern Oregon.

Representative collections: OREGON: Five miles southeast of Paisley, Lake Co., *C. L. Hitchcock No. 6574* (DS, WS).

NEVADA: Dunes north of Winnemucca, Humboldt Co., *Ripley & Barneby No. 5604* (CAS); Trinity Mts., Pershing Co., *Watson in 1868* (G, NY, US; co-types); 10 miles north of Lovelock, Pershing Co., *Train No. 35* (UN); Battle Mountain, Lander Co., *Jones in 1929* (P); between Reno and Pyramid Lake, Washoe Co., *McCracken in 1935* (CAS); Carson Sink, Churchill Co., *Eastwood & Howell No. 103* (CAS); Mountain Wells, Churchill Co., *Russell in 1929* (CAS); sandy plains north of Carson City, Ormsby Co., *Stretch in 1865* (NY; co-type); Empire City, Ormsby Co., *Torrey No. 345* (G, NY; co-types), *Jones No. 3980* (CAS, M, NY, P, US); east side of Montgomery Pass, Mineral Co., *Eastwood & Howell No. 9531* (CAS); White Mts. near Sunland, Mineral Co., *Heller No. 10512* (CAS, CM, DS, G, M, NY, US); plateau southeast of Tonopah towards Cactus Peak, Nye Co., *Ripley & Barneby No. 3726* (CAS).

CALIFORNIA: Surprise Valley, Modoc Co., *Plummer in 1879* (G); Secret Valley, Lassen Co., *Applegate No. 8928* (CAS, DS, RSA); Honey Lake Valley, Lassen Co., *Babcock & Stebbins No. 1785* (CAS); Sierra Valley, Sierra Co., *Bolander in 1872* (DS, G); Gull Lake, Mono Co., *Peirson No. 7565* (CAS, FP); Crooked Creek, Mono Co., *J. T. Howell No. 14320* (CAS, CM, M, W, WS); Owens Valley, Inyo Co., *Ripley & Barneby No. 5891* (CAS), *Eastwood & Howell No. 9556* (CAS), *Heller No. 8285* (CAS, CM, DS, G, M, NY, US); Wyman Creek, White Mts., Inyo Co., *Duran No. 3043* (CAS, CM, DS, G, M, NY, P, RM, RSA, UA, UC, US, UW); Acton, Los Angeles Co., *Elmer No. 3720* in part (CAS, DS, M, NY, P, US); 10 miles south of Muroc, Los Angeles Co., *Peirson No. 10664* (DS, FP, UC); 20 miles west of Victorville, San Bernardino Co., *Peirson No. 8919* (CAS, FP, P).

In the southern part of its distribution *P. bicolor* intergrades with *P. Fremontii* and the relationship of the two species is discussed at length under *P. Fremontii*. To the northward in central Oregon, *P. bicolor* is replaced by *P. Leibergii* which I regard as specifically distinct, although they have been generally treated as the same or as only varietally different. Whereas the intermediates between *P. bicolor* and *P. Fremontii* exhibit the fluctuating variations characteristic of a hybrid population, *P. bicolor* and *P. Leibergii* seem to be quite distinct although they are closely related. The record of *P. bicolor* from western Arizona is undoubtedly incorrect for reasons that I have discussed elsewhere (Howell, 1945a, p. 151).

9. PHACELIA LEIBERGII Brand Das Pflanzenr. IV. 251: 128 (1913)

P. bicolor Torr. var. *Leibergii* (Brand) Nels. & Macbr., Contrib. Gray Herb. n. ser. **49**:40 (1917).

P. adspersa Brand in Fedde Repert. spec. nov. **17**:319 (1921).

Root annual; stems erect or somewhat spreading, 0.5-2 dm. tall, branching at the base and above, hirsutulous and somewhat capitate-glandular below, puberulent and densely capitate-glandular above, lower internodes frequently elongate; basal leaves few, cauline leaves similar and numerous, the blades ovate in outline, 2-6 cm. long, 0.5-2.7 cm. wide, pinnately divided, the divisions oblongish, lobed or divided, the ultimate segments oblongish or deltoid-ovate, obtuse, sparsely hirsutulous above and glandular below, petioles to 2.5 cm. long; racemes not projected beyond the leafy part of the plant, becoming much elongate and to 1.5 dm. long, the lowest flowers widely distant, the uppermost crowded, pedicels 1-4 mm. long, the lowest sometimes reflexed at base; calyx-segments in flower 3-11 mm. long, 0.6-1 mm. wide, linear-oblong to narrowly oblanceolate, in fruit a little unequal, 6-13 mm. long, 0.8-1.5 mm. wide, narrowly linear-oblanceolate, the longest tending to be a little spatulate-expanded at apex, hirsutulous and glandular; corolla elongate-campanulate with "white or yellowish tube and bright blue limb" (acc. M. E. Peck), 7-13.5 mm. long, lobes 2-4 mm. long, spreading, sparsely hairy outside, minutely papillate on lobes inside; corolla-scales attached to the base of the filaments 0.5-1 mm., the scales and filaments forming a narrow pocket, the scales widest at the upper point of union with the filaments, above this point abruptly narrowed and linear-attenuate, this free part of scale 1-2 mm. long or less or even obsolete; stamens attached 0.5-1 mm. above base of corolla, somewhat unequal, the longest exserted from the corolla-throat, 5-9.5 mm. long, filaments sparsely hairy below the middle, anthers 0.5-1 mm. long; style and branches 5-8 mm. long, style hairy to above the middle, subpersistent, branches 0.33-1 mm. long; ovary 1.25 mm. long, hirsutulous, ovules 24-28; capsule oblong, 4-6 mm. long, 2-2.5 mm. wide, truncately obtuse and scarcely apiculate, the back shallowly sulcate, finely puberulent and above a little hirsutulous and more or less glandular; seeds brown, ovate, angular, rounded at base and acute at apex, 1.25-1.5 mm. long, rather shallowly corrugated, the corrugations about 10, acute with broad base.

Sandy plains of central and eastern Oregon from Crook County south to northern Lake County and east to Malheur County.

Representative collections, all from OREGON: Sage plains, *Howell in 1885* (CAS, CM, DS, G, NY, US); between Prineville and Bear Buttes, Crook Co., *Leiberg No. 321* (RM, type; CAS, CM, DS, M, NY, P); pumice desert south of Prineville, Crook Co., *Leiberg in 1894* (WS); 13 miles southeast of Bend, Deschutes Co., *Peck No. 21920* (CAS, W); Millican, Deschutes Co., *Peck No. 14312* (CAS, W); Fort Rock, Lake Co., *Peck No. 15712* (W); 9 miles south of Wagontire, Harney Co., *Peck No. 19420a* (W); near Harper Ranch, Malheur Valley, Malheur Co., *Leiberg No. 2220* (type-collection of *P. adspersa;* CM, G, NY, P, UC, US); 5 miles northwest of Harper, Malheur Co., *Peck No. 21306* (UC).

One of the chief obstacles to recognizing *P. bicolor* as a species distinct from *P. Fremontii* as far as the character of the corolla-scales was concerned

was found in the *Fremontii*-like scales which characterized the "*P. bicolor*" (i.e., *P. Leibergii*) of eastern Oregon. When it was discovered, however, that there were real differences in the stamens and styles between true *P. bicolor* and the northern plants, the confusion resolved itself in a most satisfactory manner. Not only does the segregation of *P. Leibergii* from the older inclusive interpretation of *P. bicolor* allow a clean-cut and definitive treatment of *P. bicolor* apart from *P. Fremontii*, but the specific recognition of *P. Leibergii* has disclosed the unexpected relationship between it and *P. glandulifera*.

The essential characters of both flowers and fruits in *P. Leibergii* and *P. glandulifera* emphasize a relationship so close that it might almost be treated varietally if the flowers of the two did not look so different and if each species did not have such highly characteristic geographic ranges. In fact, the more restricted range of *P. Leibergii* completely within the more extended range of *P. glandulifera* and immediately to the north of the range of *P. bicolor* strongly suggests that *P. Leibergii* may have originated long ago through hybridization between small-flowered *P. glandulifera* and large-flowered *P. bicolor*.

The characters of corolla-scales are especially valuable in *Phacelia* in interpreting relationships and broad lines of development, but, because of their variability, they must be employed cautiously and discriminately as an indication of specific or subspecific entities. Brand based *P. adspersa* on the apparent lack of corolla-scales and most erroneously allied his species to the California *P. brachyloba* in which the corolla-scales are often definitely deficient. In an isotype of *P. adspersa*, the corolla-scales are found to be much reduced but they are sufficiently developed to form with the bases of the filaments the shallow pocket characteristic of *P. Leibergii*. Above the point of union with the filaments, the scales are represented by a mere line or are quite obsolete. I do not believe this variation deserves taxonomic recognition.

The original collection of *P. Leibergii* was erroneously reported from "Washington" between "Pineville and Bear Buttes" instead of between Prineville and Bear Buttes, Oregon, (cf. Howell, 1945a, p. 150), and the type of *P. adspersa* was given from "Matthew Valley" instead of from Malheur Valley.

10. PHACELIA NEGLECTA M. E. Jones Contrib. West. Bot. 12: 50 (1908)

Plants annual, low, leafy and compactly branched, 3-10 cm. tall, the stems stout, few-branched from the base, glandular-villous but without black-headed capitate glands; leaves broadly ovate to orbicular, 0.5-3.5 cm. in diameter, thick-coriaceous, hirsutulous above and below or subglabrous above, undulate-dentate, or -crenate, sometimes with small rounded teeth alternating with the larger ones, obtuse at apex, truncate or reniform-cordate at base, petioles mostly 1-3 cm. long, thick, villous-glandular; racemes sessile, more or less concealed by the leaves, mostly short and densely flowered or the lowest flowers rather distant, pedicels thick, 1-2 cm. long, at least the lowest recurved in fruit; calyx-segments in flower 3 mm. long, 0.5-1 mm. wide, oblong or narrowly oblong, obtuse, in fruit somewhat enlarged, 5 mm. long, 1-1.5 mm. wide, glandular and hirsutulous; corolla creamy-white with yellowish veins or very pale pink, campan-

ulate, the tube nearly cylindrical, 3 mm. long, glabrous, the lobes rounded, 2 mm. long, 3 mm. wide; corolla-scales 2 mm. long, semi-linear-lanceolate, ciliate, attached at base to filaments; stamens about 3 mm. long, filaments glabrous, anthers 1 mm. long, yellow, pollen yellow; style and branches 2 mm. long, the branches 1 mm. long, the style glandular and hirsutulous; ovary 1 mm. long, densely villous-hirsutulous and a little glandular, ovules 70-104; capsule orbicular, 4 mm. in diameter; seeds a little over 1 mm. long, oblong to ovatish, mostly obtuse or obliquely truncate at ends, dark brown, corrugations about 6.

Alluvial slopes, alkaline flats, sandy washes, and desert mosaics, widely distributed but rather uncommon from Inyo County, California, south to northern Lower California and east to Clark County, Nevada, and Pima County, Arizona. No record has been seen from Sonora, Mexico, but *P. neglecta* undoubtedly grows there since a specimen has been collected in Arizona less than a mile north of the international boundary.

Representative collections: CALIFORNIA: Divide between Pahrump and Mesquite valleys, Inyo Co., *Abrams No. 14261* (DS, G); Providence Mts., 2.3 miles east of Hayden, San Bernardino Co., *Wolf No. 10737* (RSA, UC); Baker, San Bernardino Co., *Peirson No. 9834* (CAS, FP); near Barstow, San Bernardino Co., *Eastwood & Howell No. 8859* (CAS, RB); Needles, San Bernardino Co., *Jones No. 3792* (P, type; CAS, CM, G, IM); Ford's Well west of Blythe, Riverside Co., *Munz & Harwood No. 3562* (P, US); near Carrizo Mt., San Diego or Imperial Co., *T. S. Brandegee in 1905* (UC, US); Palo Verde Mts., Imperial Co., *Alexander & Kellogg No. 1957* (CAS, UC).

NEVADA: Ten miles northeast of Las Vegas, Clark Co., *Eastwood & Howell No. 8974* (CAS); Valley of Fire, Clark Co., *Clokey No. 5919* (CAS, M, NY, P, RM, UA).

ARIZONA: Lower Grand Wash, Mohave Co., *Maguire No. 20572A* (CAS, IM, UC); Yuma, Yuma Co., *Swingle No. 255* (CAS, UA); O'Neil Hills to Tule Valley, Yuma Co., *Kearney & Peebles No. 10873* (P, US); 20 miles west of Gila Bend, Maricopa Co., *Harrison & Peebles No. 9128* (S, UC, US); Pinacate Plateau, Pima Co., *Wiggins No. 6564* (DS, US); 1 mile north of Sonoyta, Pima Co., *W. B. McDougall No. 93* (UA).

LOWER CALIFORNIA: West of Indian Wells, *Orcutt No. 2035* (US).

As I indicated in my synopsis of the *P. pachyphylla* group (Howell, 1942, p. 134), *P. neglecta* is not so closely related to *P. pachyphylla* as that species is to *P. calthifolia*. These three species are distinguished by a number of such marked and peculiar characters that it is not easy to surmise their affinity to any other living phacelia. In thoughts of descent, however, it seems likely that *P. neglecta* with its less glandular vestiture, glabrous corolla-tube, and yellow anthers and pollen may be regarded as the most primitive of the three, and a vague and distant connection may be sought in *P. gymnoclada*. The remarkably distinctive difference in habit between *P. neglecta* on one hand and *P. pachyphylla* and *P. calthifolia* on the other is paralleled in habitual differences between *P. Ivesiana* and *P. affinis* and between *P. Fremontii* and *P. bicolor*.

11. PHACELIA PACHYPHYLLA Gray Proc. Amer. Acad. 19: 88 (1883)

Plants annual, disagreeably mephitic, all parts except the corolla with abundant black-headed glands intermixed with non-glandular hirsutulous hairs;

stems stout, erect, 0.5-3 dm. tall, the branches few, ascending or the lowest widely spreading; leaves thick and leathery, broadly ovate to round, mostly 1-6 cm. long and about as wide, obtuse at apex, cordate to broadly cuneate at base, undulate to crenate, plane or crisped, petioles thick, very glandular, 1-5 cm. long; racemes in 2s or 3s, borne on elongate peduncle-like branches and exceeding the leafy part of the plant, racemes 1-6 cm. long, mostly densely flowered, pedicels nearly lacking or 2-3 mm. long in the lowest flowers, spreading but not reflexed; calyx-segments in flower about equal, 3 mm. long, 0.66 mm. wide, oblong, in fruit 4.5-5 mm. long, 1 mm. wide, oblongish but a little wider near the base, densely glandular and hirsutulous; corolla open-campanulate, pale violet, 5-6.5 mm. long, the lobes 3 mm. long, rounded, entire, the upper part of the tube hairy inside; corolla-scales narrowly linear-deltoid, 1-2 mm. long, thick, densely long-ciliate, attached at very base to broadened base of filaments; stamens a little unequal, 2.5-4 mm. long, the anthers 1 mm. long, violet, pollen lavender, the filaments glabrous, 2.5-3.5 mm. long; style and branches 2-2.5 mm. long, the branches 1-1.25 mm. long, the style glandular and hirsutulous up to the branches; ovary 1 mm. long, glandular-hairy, ovules 48-114; capsule plumply ovate to orbicular, 5-7 mm. long, 5 mm. wide, capitate-glandular and hirsutulous, the styles persistent as a prominent apiculation 1 mm. long, the valves prominently sulcate; seeds angular, with about 6 or 7 corrugations, a little over 1 mm. long, brown, the ends pointed or obliquely truncate.

A rather uncommon plant of the Mohave and Colorado deserts in California, growing on alkaline flats and slopes and especially characteristic of "desert mosaics," San Bernardino and Kern counties southward to Imperial County.

Representative collections, all from CALIFORNIA: Red Rock Canyon, Kern Co., *J. T. Howell No. 4924* (CAS, CM, G, NY, RSA, S, US); Petrified Forest Canyon, Kern Co., *Peirson No. 7342* (CAS,FP); 12 miles east of Lucerne Valley, San Bernardino Co., *Munz & Youngberg No. 15162* (CAS, M, P, RM, UC); dry alkaline lake near Calico, San Bernardino Co., *S. B. & W. F. Parish No. 1313* (G, type; CM, DS, US); near Barstow, San Bernardino Co., *Eastwood & Howell No. 8821* (CAS), *No. 8869* (CAS), *Peirson No. 7291* (CAS, FP, P); near Manix, San Bernardino Co., *Eastwood & Howell No. 8883* (CAS); near Paloverde, Riverside Co., *Creata & Hall No. 5955* in part (DS); Painted Gorge, Imperial Co., *Peirson No. 13072* (FP, UC), *Ferris & Rossbach No. 9602* (DS).

In his recent treatment of California phacelias, Jepson (1943, pp. 280, 281) describes *P. neglecta* M. E. Jones ("a low dwarf 1 to 2½ inches high") under the name of *P. pachyphylla*, while specimens of this species he segregates among his citations as "loosely branching forms 2 to 5 inches high." After observing the differences between the two plants as they grew together east of Barstow without the faintest indication of intergrading, I am convinced that *P. pachyphylla* and *P. neglecta* represent two species as distinct as any in *Phacelia* sect. *Euglypta* (cf. Howell, 1942, pp. 133, 134).

12. PHACELIA CALTHIFOLIA Brand Beilage, Jahresb. Kgl. Gymnas. Sorau 8 (1911)

Plant annual, abundantly capitate-glandular and hirsutulous, the stems stout, erect, 1.5-3 dm. tall, rarely lower, branching above, the branches few,

peduncle-like; leaves broadly ovate to round, 2-12 cm. long, thick, heavily glandular, rather irregularly crenate or dentate, obtuse at apex, cordate to broadly cuneate at base, petioles thick and very glandular, to 8 cm. long, the uppermost leaves much reduced and nearly sessile, racemes usually paired or in 3s, borne on peduncle-like branches above the leafy part of the plant, flowers distant below, crowded above, pedicels 1-2 mm. long below, shorter above, the lowest spreading or recurved; calyx-segments oblong, 3.5 mm. long, 0.6-1 mm. wide, not much enlarging in fruit, becoming 4.5-5 mm. long, hairy and glandular; corolla broadly campanulate or subrotate, purplish, 8-12 mm. long, the tube hairy inside, lobes rounded, 4-6 mm. long and wide; corolla-scales 2-3 mm. long, semi-ovate or semi-lanceolate, hairy and ciliate, the lowest part attached to base of filaments about 0.5 mm. or more; stamens a little unequal, 5-6 mm. long, the filaments purplish, glabrous, anthers about 2 mm. long, violet, pollen lavender; style and branches 5-6 mm. long, the branches 2.5-4 mm. long, the style and base of branches hirsutulous; ovary 1 mm. long, hairy, ovules about 50; capsule plumply oblong or globose, 4-5 mm. long, obtuse with a conspicuous beak, capitate-glandular and hirsutulous; seeds 1-1.3 mm. long, ovate to elliptic, angular, acute at apex, brown, corrugations about 7.

Argillaceous soil of silted flats and detrital slopes below canyon walls, in the region centering in Death Valley, Inyo County, California, extending southward to San Bernardino County and eastward to the adjacent part of Nye County, Nevada.

Representative collections: NEVADA: Amargosa Desert, Nye Co., *Jones in 1907* (CAS, DS, M, P, US).

CALIFORNIA: Shoshone, Inyo Co., *E. R. Johnson in 1928* (CAS, DS, RSA); Furnace Creek Wash near Ryan, Inyo Co., *J. T. Howell No. 3674* (CAS); Golden Canyon, Death Valley, *Eastwood & Howell No. 7721* (CAS); Pleasant Canyon, Panamint Mts., Inyo Co., *Hall & Chandler No. 6932* (UC, type; G); Panamint Canyon, Panamint Mts., Inyo Co., *Jones in 1897* (CAS, DS, G, IM, M, P, RM, US); Willow Spring, Saline Valley, Inyo Co., *Kerr in 1940* (CAS, CM, UN, WS); 37 miles north of Baker, San Bernardino Co., *J. T. Howell No. 3600* (CAS); Baker, San Bernardino Co., *Peirson No. 9837* (FP); 11 miles east of Ludlow, San Bernardino Co., *Wiegand & Upton No. 4089* (CM).

Phacelia calthifolia is one of the remarkable phacelias that are nearly confined to the Death Valley region, but unlike the other endemics, *P. perityloides* Cov. and *P. mustelina* Cov., it is a more common plant and is even quite abundant following a season of plentiful rainfall. M. E. Jones distributed his 1897 collection of the species with a name he never published because he came to regard the Death Valley plant as merely a large-flowered phase of *P. pachyphylla* Gray (cf. Jones, 1908, p. 51). As far as relationship is concerned Jones was right in recognizing the affinity of the two species, but certainly *P. calthifolia* is an excellent species, well distinguished from *P. pachyphylla* by numerous characters of flower and fruit.

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Ficus in Florida—I. Australian Species

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Introduction

Most species of the enormous genus *Ficus* seem to have fairly rigid continental limits so far as their natural distribution is concerned. Florida, however, particularly in those sections south of a line from Vero Beach on the east to Clearwater on the west, offers impartially a home to certain African, Asian, Australian, and Central and South American species in addition to its native fig-trees, *Ficus aurea* Nutt. and *F. brevifolia* Nutt.

The exhibits in this informal state museum are concentrated in such places as Chapman Field, the plant introduction station of the United States Department of Agriculture located about seven miles south of Coconut Grove, in the McKee Jungle Gardens near Vero Beach, and in various nurseries: for example, the Royal Palm Nurseries near Oneco. They also are scattered throughout the area in parks, along roadsides, and on private estates. Some specimens still are small and have borne no fruit. Others, especially those planted years ago for their decorative value in Coconut Grove, Fort Myers, Punta Gorda and other places, have attained large size.

Since the identity of most of these specimens is known, and because some of the species need new descriptions and their nomenclature requires renovation, the opportunity of combining field, herbarium and library investigations of trees and shrubs normally widely scattered has seemed one which should not be neglected.

The principal objects of the following studies of Australian species of *Ficus* which have been introduced into Florida are: emphasis on correct names, according to the international rules of botanical nomenclature; collection and evaluation of alleged synonyms; descriptions from literature and first-hand observations; and location of specimens in Florida.

The field observations have been made in many places from the Vero Beach-Clearwater line south as far as Chapman Field. This last station has by far the greatest numbers and varieties of *Ficus*. The herbaria consulted are those of the New York Botanical Garden; the Arnold Arboretum of Harvard University at Jamaica Plain, Massachusetts; the Florida Agricultural Experiment Station at Gainesville, Florida; and the United States National Herbarium, Washington, D.C. The library work has been done mostly at the New York Botanical Garden, but also at the Arnold Arboretum. To those in charge of the plants and herbaria, and on the library staffs of the above institutions I want to express my thanks. I am grateful also to the persons who have acted as advisers, or as guides to public and private collections of *Ficus*: particularly to the late Dr. John Kunkel Small, formerly of the New York Botanical Garden; to Mrs. Charles T. Simpson, Mrs. Young C. Lott and Mr. Karl Dahlberg of Miami; to Mrs. Marian A. McAdow of Osprey, Florida; to

Messrs. Jens Hansen and Henry Hoffman of the McKee Jungle Gardens, and to Mr. James A. Combs, formerly of the Royal Palm Nurseries, Oneco.

Ficus rubiginosa

FICUS RUBIGINOSA Desfontaines ex Ventenat, Jard. Malmaison 2: 114. *pl. 114.* 1805.*

F. australis Willd. Sp. Pl. **4**:1138. 1806. *F. ferruginea* Desf. Cat. Pl. Hort. Reg. ed. 3: 413. 1829. *Mastosuke rubiginosa* (Desf. ex Vent.) Raf. Syl. Tell. 59. 1838. *Urostigma rubiginosum* (Desf. ex Vent.) Gasp. Nov. Gen. Fic. **7**:1844. *F. fulva* Hort. Berol. 1846 ex Kunth, Ind. Sem. Hort. Berol. 1846. 14. 1846. *U. ferrugineum* (Desf.) Miq. Hook. London Jour. Bot. **6**:534. 1847.

F. rubiginosa (Desf. ex Vent.) var. *variegata* Guilfoyle, Australian plants 178. 1911. *F. rubiginosa* (Desf. ex Vent.) var. *glabrescens* F. M. Bailey, Comp. Cat. Queensland Pl. 486. *pl. 477*2. 1913.

TYPE: cultivated in the garden of Malmaison, France.

Distribution: Australia: Queensland, New South Wales. New Caledonia. Widely cultivated on other continents.

Common names: Rusty, Port Jackson, small-leaved, southern, and Illawarra fig; Botany Bay fig tree, Rusty-leaved India rubber plant.

Reported as a large Australian tree of banyan type; in Florida a small tree with aerial roots. Twigs, buds, petioles, under surface of leaf blades, and figs rusty-hairy, becoming almost or quite bare. Petioles 2.5-4 cm. long. Blades leathery: ovate to elliptical or oblong; 7-14.5 cm. long, 3.5-8.5 cm. wide (examples: 9.5 x 5.5, 10.5 x 5.5, 12 x 6 cm.); apex slightly narrowed, usually obtuse, rarely short-acuminate; base rounded or subcordate; margin entire; upper surface glossy dark green, pustulate in old age; lower surface brownish, velvety to bare; one or more sets of basal veins, the more distinct forming an angle of about 90°; usually 7-11 sets of secondary lateral veins, each vein with an upper angle of about 50°; one main tertiary vein between and parallel to each two successive secondaries, forming with them an indented intramarginal vein; reticulum rather indistinct; background checkered; a gland at junction of midrib and petiole. Figs axillary, typically paired, globose or ovoid, 1-1.5 cm. in longer diameter, showing dots or warts or ribs when bare, apex obtusely umbonate with protruding bracts; basal involucre hairy, bracts deciduous; peduncle 2-7 mm. long, thick. Male and female flowers said to be intermixed and to have 3 oval perianth parts rounded at apex; one stamen, filament short, anther reniform; an ovoid, pedicelled ovary, and a lateral, filiform style with a short, linear, acute stigma.

Commentary

Living plants of this fig-tree were sent by Sir Joseph Banks in 1789 from New South Wales to the Royal Gardens in England. That other specimens were received then or later by botanical gardens in France, Italy and Germany is evident from the origin of much of the synonymy.

* See Stearn, Jour. Arnold Arb. **23**:110 (foot-note), 1942 for statement on 1805 as the publication date of this plate.

The name *Ficus rubiginosa* was given without adequate description to specimens from "New Holland" (Australia) by Desfontaines, Tabl. ed. 1: 209. 1804. In 1805 Ventenat described and illustrated the species, citing *F. rubiginosa* Desf. as authority. Although Desfontaines' title was *nomen nudum* it has frequently been used under his authorship. However, Desfontaines credited it to Ventenat by quoting, Hist. arbres 2: 410. *pl.* 2. 1809 from his description, and later by citing him as author, in Tabl. ed. 2: 239. 1815, and Cat. Pl. Hort. Reg. ed. 3: 346. 1829. A number of other writers have accepted Ventenat's authorship, but few have associated both botanists.

Willdenow name, *F. australis,* has been employed by several authors. He cited *F. rubiginosa* Desf. as a synonym and New Holland as the distribution, but apparently described the species from specimens in the Berlin Royal Garden. (See also Willd. Enum. 1063. 1809, and Kunth, Ind. Sem. Hort. Berol. 1846: 17. 1946.)

F. ferruginea has been reported from several different places, usually in connection with *F. rubiginosa.*

F. ferruginea Hort. was listed by Colla, Hort. Ripulensis 55. 1824, as a synonym of *F. australis* Willd. Another plant reported as *F. ferruginea* Hort. was cited by W. J. Hooker, Curtis's Bot. Mag. **56**: no. 2939. 1829, as a synonym of *F. rubiginosa* Desf. This probably was a fruiting specimen which had been sent in 1827 from the Liverpool Garden to the British Royal Gardens. (See also Miquel, Hook. London Jour. Bot. **6**: 561. 1847.)

F. ferruginea was first validly published when Desfontaines described plants under that name, from the Royal Garden at Paris, declaring that the species was distinct from *F. rubiginosa* Vent. On a previous page (p. 346) he had listed without description both *F. ferruginea* Parmentier and *F. rubiginosa* Vent. Apparently Parmentier was not an author, for he is not so cited in the description. Bureau, Ann. Sci. Nat. V, **14**: 249. 1872, has believed the two species to be the same. The principal differences seem to lie in the very large, obtusely acuminate leaf blades of *F. ferruginea.* These correspond in size of blade to the leaves of *F. columnaris* Moore & Muell. but lack the very long petioles of that tree. Short, blunt leaf tips have been reported by Francis, Australian rain-forest trees 69. 1929, for *F. rubiginosa.* If *F. ferruginea* Desf. is accepted as a synonym it carries with it *Urostigma ferrugineum* (Desf.) Miq., and also the invalidly published *F. fulva* Hort. Berol. 1846, which Kunth, above, p. 14, declared was a synonym of *F. ferruginea* Desf.

F. ferruginea Hort. ex Miq. in Mart. Fl. Brasiliensis **41**: 93. 1853 belongs to a different species.

The generic names *Mastosuke* and *Urostigma* exemplify attempts to break up the enormous genus *Ficus.* The former has long since been abandoned, and *Urostigma* exists only as a sub-genus of *Ficus.*

Of variety *variegata* Guilfoyle said that the Variegated Port Jackson Fig from New South Wales was evergreen and 3.7-4.6 m. high. The pattern of the leaf surface may be assumed from the name.

F. M. Bailey's plate and brief description of variety *glabrescens* from

Queensland indicate smaller figs and more or less glabrous leaves which are smaller and more pointed than those which he illustrates of Queensland specimens of the type. But even smaller and more pointed glabrescent leaves were found by me in Florida on *F. rubiginosa*. In the absence of specimens and additional references the authenticity of this variety remains uncertain.

Summary

The authorship of *F. rubiginosa* has been ascribed to Desfontaines or to Ventenat, but should be written as Desf. ex Vent. The species often has been called *F. australis* Willd. or *Urostigma rubiginosum* Gasp.

The tree may be recognized especially by the rusty-hairiness of young parts, by medium-sized blunt leaves whose length is about twice their width and whose secondary side veins average about 1 cm. apart, by rather short petioles, and by usually ovoid, eventually rough figs 1 cm. or more long, on short thick peduncles.

Among the synonyms are *Mastosuke rubiginosum* (Desf. ex Vent.) Raf., *F. ferruginea* Desf., and *Urostigma ferrugineum* (Desf.) Miq. Little-known varieties are *variegata* Guilfoyle, and *glabrescens* F. M. Bailey.

Useful references not previously listed are: F. M. Bailey, Queensland Fl. 5: 1466, 1471. 1902; Bentham, Fl. Australiensis 6: 168. 173; Maiden, various texts; H. Mowry, Orn. trees, Florida Agr. Ext. Bull. 95. *pl. 42*. Ap. 1938; Nehrling, Plant World Florida 179. 1933.

Living specimens have been studied by me at Chapman Field, on the estate of Mrs. Charles T. Simpson in Miami and at the Royal Palm Nurseries.

Ficus watkinsiana

FICUS WATKINSIANA F. M. Bailey, Queensland Dept. Agr. Bot. Bull. 2: 18. 1891.

F. bellingeri C. Moore, Handb. Fl. New South Wales 81. 1893.

In Australia said to be a glabrous evergreen tree to 20 m. high; trunk to 2 m. diameter, sometimes surrounding remains of trunk of host plant, bulging at base; aerial and prop roots sometimes present; bark light-colored, longitudinally filigree-wrinkled in young tree, not scaly; twigs stout, green-glaucous or sometimes hairy at first, becoming bare and rough; stipules of terminal buds 5-7.5 or 9.5 cm. long, narrow, gradually acuminate, becoming bare, reddish; petioles 4-7 cm. long, slender, slightly hairy to bare; blades 10-20 x 5-9 cm. (examples: 13 x 6, 15 x 5 cm.); narrow-ovate, elliptical or elliptical-lanceolate; thin-leathery; apex gradually narrowed into a sharp to blunt tip or a very short acumen; base slightly tapering; margin entire; upper surface glabrous, dark green; under surface yellow-green; a gland near base of midrib; usually one pair of basal veins, of about the same thickness as the secondary veins, making a basal angle of 80°-100°; 14-20 sets of secondary lateral veins, upper angle 65°-80°, forking and forming a scalloped intramarginal vein; usually one prominent tertiary vein between consecutive secondaries; reticulum and checkered background present; figs axillary, paired at first, oblong-ovoid with an

abruptly narrowed and umbonate apex 2.5-4.5 x 1.5-3 cm. in size, greenish to deep purple, bearing wart-like spots, base resting on a cartilaginous disk 1-1.7 cm. in diameter, formed by the basal bracts; peduncle 1.5-2.5 cm. long, thick, widest at tip; male flowers said to measure 1.5-3.5 mm., long-pedicelled; perianth parts 4, ovate, subacute, about 1 mm. long; one stamen with a short filament and a reniform anther; female flowers sessile; perianth parts 4, linear, wider at base than at apex, shorter than ovary; ovary ellipsoid, 2-5 mm. long; style lateral, 2 mm. long, filiform; gall flowers like the female, but with a shorter style and a capitate stigma.

TYPE: Queensland. *H. Tryon. Alex. Anderson.*

Distribution: Australia: New South Wales, Queensland.

Common names: Watkin's fig tree. Bellinger River fig tree.

Commentary

Francis (Australian Rain-forest trees 69. *pl. 33.* 1929.) and Summerhayes (*in* Hooker's Icones plantarum 32: *pl. 3187.* 1933) believed *F. bellingeri* to be a synonym of *F. watkinsiana*. The only difference between living specimens of the two, as seen by me at Chapman Field, was a slight hairiness of young buds, twigs and petioles of the tree labeled *F. bellingeri*. Its figs were like those of herbarium specimens of *F. watkinsiana* seen by me at the Arnold Arboretum and at the New York Botanical Garden, and like those of the plates of Francis and of Summerhayes.

G. R. Wilson (Proc. Florida Hort. Soc. 1937: 66. 1938) has recommended *F. watkinsiana* tentatively for southern Florida.

Summary

Distinguishing characters of *F. watkinsiana* (formerly known also as *F. bellingeri*) are its medium large, rather narrow, glabrous leaf blade, narrowed at both ends and showing many parallel secondary and tertiary veins; and its large, ovoid, spotted, umbonate fig resting on a cartilaginous disk at the apex of the peduncle. The tree has been grown in southern Florida.

Ficus stephanocarpa

In 1905 Warburg gave the name *Ficus stephanocarpa* to an Australian fig tree which for years had been incorrectly called *F. aspera* Forst. f. and *F. scabra* Forst. f. His determination was the result of his examination of Forster's original specimens of *F. aspera*, and of other specimens which Seemann (see below) believed to be of the same species as Forster's *F. scabra*. Warburg added that *F. stephanocarpa* had been known in some botanical gardens as *F. exasperata* Vahl, and as *F. ulmifolia* Lam., and also that it differed from *F. coronulata* Miq.

Since in recent years I have seen living and herbarium specimens of *F. stephanocarpa* which were labeled *F. aspera*, and since Domin (Bibl. Bot. 89: 568. 1921) found that the species continued to be called *F. aspera* and *F. scabra* after Warburg's differentiation of it, I have thought it worth while

to add somewhat to Warburg's description of *F. stephanocarpa,* to compare it with the other species mentioned by him, to trace the course of its confusion with *F. aspera* and *F. scabra,* and to list references additional to those summarized by Domin.

FICUS STEPHANOCARPA Warb. Fedde, Repert. 1: 75. 1905.

F. aspera of F. M. Bailey, Bentham, Guilfoyle, Maiden, Miquel, Mueller, and Simmonds; not of Blanco, or Forster f. *F. scabra* of F. M. Bailey, Ewart & Davies, Maiden, C. Moore, Mueller, and Renner; not of Blanco, Forster f., Jacquin, Sim, or Willdenow.

In Australia reported to be bushy or a tree 15-30 m. high, in Florida a small, rather straggling tree; twigs hairy and hispid to bare and rough; stipules linear, pubescent, acute, about 8 mm. long at first, deciduous; petioles from 3 mm. long, stout, hairy, rough; leaf blades lanceolate to elliptical; thin; 6-15 x 3-6.5 cm. (examples: 12 x 4 cm., 10 x 3.5 cm., 7.5 x 3.3 cm.); apex acute, sometimes prolonged; base obliquely subcordate or rounded; margin toothed or shallow-sinuate; upper surface rough, lower surface white-hairy to almost bare; angle of large basal veins with each other 30°-40°, of lateral secondary veins 60° or more; 6 or 7 distinct sets of secondary veins, curved near midrib, confluent near margin; no tertiary veins; distinct coarse reticulum; figs axillary, said to grow also from trunk and main branches, paired at first, ovoid or ellipsoid, pale-hairy, about 1 cm. long, red to purple when ripe; peduncle 2-9 mm. long, hispid; basal bracts lanceolate, small, hispid, deciduous; apical bracts in several rows, erect, forming crown, lanceolate, 2-3 mm. long, pubescent; report (Warburg's) of flowers showing male and gall flowers in one set of receptacles, females in another set; male flowers clustered near the ostiole, lobes of perianth almost free, glabrous, oblong, scarcely hooded; one stamen; lobes of perianth in gall and female flowers oblong, obtuse; style of gall flowers short, glabrous, thickened at the barely capitate apex; style of female flowers long; stigma long, papillose, not thickened.

TYPE: Toowoomba, Queensland, Australia. Scrub. *Warburg no. 18478.*

Distribution: Australia: Queensland, New South Wales, Northern Territory.

Common Names: Rough, purple, tongue-leaved, sandpaper, creek or white Fig.

Comparisons

The six rather variable species mentioned by Warburg resemble one another in their rough, acute, generally oblique and more or less hairy leaf blades, which usually have a toothed or wavy margin. The figs show apical bracts.

F. aspera Forst. f. Pl. Esc. 36. 1786 was described from Tanna Island in the New Hebrides, and has since been found elsewhere in that group and in Fiji. Fijian specimens have been characterized by Seemann (Fl. Vitiensis 249-250. 1865-1873) and illustrated in color by Walter Fitch in that book (*pl.* 65). Warburg (above, p. 76) has a note on its characters.

The species is distinguished by its large, ovate, sinuate rather than toothed leaves, which may measure 18 x 8 cm.; and by its globose figs, about 1.5 cm. in diameter, with peduncles of about the same length. Only the tips of the apical bracts are visible.

F. scabra Forst. f. Prodr. 76. 1786 was described from Tanna and Namoka Islands in the New Hebrides, and has since been reported from the Tongan, Fijian and Samoan Islands. Seemann (above, p. 249, *pl. 64*) also has characterized this species, and has had it illustrated.

The leaves of *F. scabra* differ little from those of *F. aspera*, and consequently are unlike those of *F. stephanocarpa*. Its figs resemble, to some extent, those of Warburg's species, but are more nearly globose, and lack the erect crown.

No botanical gardens containing *F. exasperata* and *F. ulmifolia* were located by Warburg. These unimportant horticultural names were cited by Miquel (Ann. Mus. Bot. Ludg. -Bat. 3: 291. 1867) as located respectively at Kew and Berlin. He used them as synonyms of *F. aspera* Forst. f., referring to his own description (*in* Hook. Lond. Jour. Bot. 7: 425. 1848) of an Australian tree which he called by that name. This description shows by its characters of "oblong," narrow, few-veined leaves, and globose-urceolate figs with erect apical scales that it probably belongs to *F. stephanocarpa*.

I have seen no other reference to *F. exasperata* Hort. Kew 1847. *F. exasperata* Vahl, En. Pl. 2: 197. 1806 is an African and Arabian species, not reported from Australia by its author or by such writers on African plants as Mildbraed and Burret (Engl. Bot. Jahrb. 46: 200. 1911) and Hutchinson (*in* Prain, Fl. Trop. Africa 6^2: 111. 1916). It must be admitted that descriptions and plates of *F. exasperata* Vahl by Miquel (Hook. Lond. Jour. Bot. 7: *pl. 14 C*. 1848) and in Colla's Hort. Ripulensis, *pl. 8*. 1824 (under the name *F. coronata* de Spin) resemble *F. stephanocarpa* to some extent, except for the lower part of the receptacle, which tapers into a stalk divided from the peduncle by basal bracts.

F. ulmifolia Lam. Enc. Meth. 2: 499. 1788 has been described and its synonymy stated by Merrill (various publications, including Enum. Philippine Fl. Pl. 2: 67. 1923. It is usually not a tree, has leaves varying from simple to lobed, and figs which tend to be globose, and measure 1.5 cm. in diameter. Its distribution, as listed by Merrill, is confined to the Philippines. The *F. ulmifolia* of the Berlin Garden was probably that mentioned by Kunth (Ind. Sem. Hort. Berol. 1846: 21. 1846, and Ann. Sci. Nat. III, 7: 254. 1847). The size of the fig is not given and the description might apply to either *F. ulmifolia* Lam. or *F. stephanocarpa*.

F. coronulata Miq. Jour. Bot. Neer. 1: 242. 1861 was based upon specimens of F. v. Mueller's from Arnhemsland in Australia. The original description reads much like one of *F. stephanocarpa;* but Warburg states that the species is different and is characterized by narrow, many-veined, scarcely rough leaves, and by figs with long bare peduncles.

Course of the Confusion

Miquel (above, 1848) seems to have been the first to apply the name *F. aspera* to an Australian species. He listed locations of specimens as Tanna, and Brisbane River (Australia) where it had been collected by Cunningham. Seemann (above) cited Brisbane River, Cunningham, collector, as one location

for the true *F. aspera* Forst. f., although on pp. XXI and XXII he had said that "Vitian" (Fijian) phanerogams do not contain a single species which is of genuine "New Holland" (Australian) type, and he also had listed no *Ficus* common to the two regions. Thereafter the present *F. stephanocarpa* was reported in Australia as *F. aspera* by Mueller through 1868, Bentham in 1873, F. M. Bailey through 1890, Maiden through 1889 and others.

The name *F. scabra* was adopted for the Australian tree instead of, or sometimes in addition to *F. aspera* by Mueller through 1889, Maiden through 1893, Charles Moore in 1893, F. M. Bailey through 1913, Ewart & Davies in 1917, and others.

References Additional to Those Cited by Domin

F. aspera. Miquel in Hook. Lond. Jour. Bot. 7: 425. 1848; Ann. Mus. Bot. Lugd. -Bat. 3: 291. 1867. Nilson, Timb. Trees N. S. Wales 78. 1884. Guilfoyle, Australian Plants 177. *pl. p. 184.* 1911.

F. scabra. Renner, Engl. Bot. Jahrb. 39: 396. 1907.

F. stephanocarpa Warb. Maiden & Betche, Cens. N. S. Wales 55. 1916. Francis, Australian Rain-for. Trees 69. 1929.

Summary

According to the interpretation given by Warburg and accepted by Domin, Maiden & Betche, Francis and others the name *F. stephanocarpa* should be used for an Australian fig tree with white-hairiness on leaves and figs, with more or less toothed, narrow elliptical or lanceolate, rough leaves, and with ovoid, pedunculate figs bearing an erect crown of several rows of lanceolate apical bracts.

F. stephanocarpa was called *F. aspera* through three-quarters of the 19th century. Then, well into the 20th century, both *F. aspera* and *F. scabra* were employed as titles. The species has received the names *F. exasperata* and *F. ulmifolia*, in botanical gardens, and needs also to be differentiated from *F. coronulata* Miq.

From the first four of the following species *F. stephanocarpa* is separated by its distribution. In addition it differs from *F. aspera* Forst. f. in its smaller, narrower leaves, and smaller, ovoid figs with an erect apical crown; from *F. scabra* Forst. f. in smaller, narrower leaves, and white-hairy, less globose figs, with an erect apical crown; from *F. exasperata* Vahl. in usually larger leaves and unstalked (although pedunculate) figs; from *F. ulmifolia* Lam. in unlobed leaves and smaller figs; and from *F. coronulata* Miq. in rough leaves and shorter, hispid peduncles.

A few references which seem to refer to this tree have been added to Domin's list. A living tree labeled *F. aspera* was studied in Chapman Field.

Ficus macrophylla

Ficus macrophylla Desf. ex Pers. has been planted on lawns and along streets in Fort Myers, Punta Gorda, Sarasota Beach, Coconut Grove and

other places in Florida. It is well spoken of by Mowry (Florida Agr. Ext. Bull. no. 95: 52. *pl. 41*. 1938), Nehrling (My Gard. Florida 201, 293, 317, 323, 333-334. 1944), Simpson (Orn. Gard. Florida ed. 1: 135. 1916), and the Royal Palm Nurseries (Trop. Pl. Book 15. [1938]); although G. R. Wilson (Florida Hort. Soc. Proc. 1937: 67. 1938) has suggested that it may do better in other places than on the limestone of Coral Gables.

FICUS MACROPHYLLA Desfontaines ex Persoon, Syn. Pl. 2: 609. 1807. (Not of Roxburgh or Link).

F. macrophylla Desf. Tabl. ed. 1: 209. 1804. (Nomen nudum). *F. huegelii* Kunth & Bouché, Ind. Sem. Hort. Berol. 1846: 15. 1846. *F. macrocarpa* Huegel ex Kunth, Ind. Sem. Hort. Berol. 1846: 15. 1846. (Not of Blume, Garparrini, or Wight ex Miquel). *Urostigma macrophyllum* (Desf. ex Pers.) Miq. Hook. Lond. Journ. Bot. **6**: 560. 1847. *U. huegelii* (Kunth & Bouché) Miq. Hook. Lond. Journ. Bot. **6**:586. 1847. *U. squamellosum* Miq. Journ. Bot. Néer. **1**:239. 1861. *F. squamellosa* (Miq.) Miq. Ann. Mus. Bot. Lugd. -Bat. **3**:287. 1867. *F. magnolioides* Borzi, Boll. Ort. Bot. Palermo **1**:47. 1897. *F. magnolioides* var. *macrophylla* Borzi, Boll. Ort. Bot. Palermo **1**:47. 1897. *F. nervosa* Haenke ex Borzi, Boll. Ort. Bot. Palermo **1**:47. 1897.

Said to be, in Australia, a very large tree to 60 m. high; in Florida large, rapidly growing; trunk deeply ridged, thick if tree starts as an epiphyte, often with buttresses extending to several meters from its base; crown large, dense; aerial roots often present, but not always reaching the ground; bark gray to black, rough or scaly; twigs thick, bare, scars pinkish when fresh; terminal bud long-conical, straight; its stipules lanceolate, acute, pinkish, downy to bare, sometimes greatly elongating, deciduous; petioles rather stout, bare, 4-9 cm. long (usually 6-7 cm.) leaf blades ovate or elliptical, 15-30 x 7.6-15 cm. (examples 24 x 10, 20 x 9, 17 x 8.5 cm.), leathery; apex usually tapering to an acute to blunt tip, rarely very short acuminate; base rounded or wide-cuneate, rarely subcordate, bearing a gland on the under surface of the midrib; margin entire, sometimes revolute; upper surface shining yellow- to dark-green; under surface silvery at first, becoming brownish or rusty-dotted; midrib prominent, lighter in color than other veins; at least one distinct pair of basal veins, forming an angle of about 90°; 12-22 sets of parallel secondary lateral veins, upper angle at midrib 60°-80°, forking and uniting to form a scalloped intramarginal vein 2-4 mm. from the margin; at least one tertiary vein between consecutive secondaries; reticulum and checkered background present; figs axillary, globose or slightly ovoid, 2-2.5 cm in diameter, or with a width of 1.5 to 2.5 cm., dark reddish-brown or purple with lighter colored spots, bare or downy; apex rounded; basal bracts slender, downy, deciduous; peduncles 1.5-2.5 cm. long, downy, slightly enlarged at apex; reports of flowers stating male, female and gall flowers to be together in receptacles (sub-genus *Urostigma*); flowers short-pedicelled or almost sessile; male perianth parts 3 or 4, short, ovate, obtuse; a single stamen with a very short filament or none, anther broad ovate; female perianth parts ovate, acute; style basic; stigma clavate or truncate.

TYPE: Australian tree cultivated in the Royal Garden, Paris.

Distribution: Australia: New South Wales, Queensland. Cultivated elsewhere in botanical gardens, and in California and Florida.

Common Names: Moreton Bay, Large-leaved, Long-leaved or Black Fig.

Economic Importance: trees for shade and ornament, wood handsome but hard to season, fiber for mats, latex for rubber, leaves for food of stock.

Nomenclature

The authorship of this species has been variously ascribed to Desfontaines, Persoon, Desfontaines in Persoon, or Desfontaines ex Persoon; and therefore needs explanation.

Desfontaines' name, *Ficus macrophylla*, was *nomen nudum* because it was listed without adequate description in his *Tableau de l'école de botanique*. In this book's preface, page V, Desfontaines said that he would give for each plant its Latin and French names, its location on the premises of the Natural History Museum of Paris, and a symbol (for example, to denote the habit of the stem). Consequently he stated of *F. macrophylla* only that it came from New Holland (Australia), was woody, and could be found in the Orangerie. A later book, he promised, would contain short descriptions.

The volume of descriptions was not published until 1829. It bore the title *Catalogus plantarum horti regii parisiensis, ed. 3*, and evidently was considered to be the third edition of *Tableau*, since a second edition of that work, issued in 1815, was the only other book by Desfontaines. In the meantime Persoon, although he did not mention Desfontaines, had described the same species. This is shown by his use of the specific name *macrophylla*, of the New Holland location, and of the initials H. P. as source. These apparently stood for *Hortus parisiensis*. Furthermore, Desfontaines' *Catalogus*, p. 412, listed Persoon as the author of *F. macrophylla*. Therefore the authorship should be written as Desfontaines ex Persoon.

Miquel was responsible for the recognition of the two series, *huegelii* and *squamellosa*, as synonyms of *F. macrophylla*. Specimens in the Berlin Garden which Huegel had called *F. macrocarpa* were re-named *F. huegelii* by Kunth and Bouché because *macrocarpa* had been used in 1825 by Blume for a different species. In 1847 Miquel transferred both *F. huegelii*, with its synonym *F. macrocarpa*, and *F. macrophylla* to Gasparrini's genus *Urostigma*. In 1861 (Iour. Bot. Néer. 1: 235) he stated that *U. huegelii* was a synonym of *U. macrophyllum*, and in the same book he described *U. squamellosum* from Australia. In 1867 (Ann. Mus. Bot. Ludg. Bat. 3: 267) Miquel returned *macrophyllum* to *Ficus* and said that *U. squamellosum* was a small form. On p. 287 of the same volume he mentioned *F. squamellosa* as forma *minor*.

One of the best descriptions of *F. macrophylla* is Borzì's of *F. magnolioides*. This synonym carries with it the name *F. nervosa* Haenke, which Borzi said was the title of *F. magnolioides* in the register of the garden in the south of France from which a specimen was brought to Palermo in the middle of the nineteenth century.

Most of the above synonyms are vouched for by Warburg (Fedde, Repert. 1: 73. 1905) and Domin (Bibl. Bot. 89: 566. 1921).

Alleged Variations

F. magnolioides var. *macrophylla* Borzì. This variety was distinguished from the type by its broader leaves: that is, wider than 10-12.5 cm. But such widths have occasionally been reported for the type by other writers, and are not inconceivable in plants under cultivation, as in Palermo.

F. macrophylla var. *pubescens* F. M. Bailey, Queensland Agr. Jour. 26: 316. *pl. 33.* 1911. I have not seen the original text and plate; but the former was quoted in Fedde, Repert. 13: 495. 1915, and a description and illustration are to be found in Bailey, Compr. Cat. Queensland Pl. 487, *pl 484.* 1913. The author said the variety was often mistaken for the type near Brisbane (Queensland).

The principal differences from the type are the brown hairiness of the tree and the disk of basal bracts which Bailey's *plate 484* shows. The fig was said to be ovoid or bluntly three-sided. Bailey thought that the tree might represent a distinct species and Domin (above, p. 567) believed this to be true. He has named the plant *F. baileyana,* since *pubescens* had been used before for a different species.

Miquel's forma *minor* had petioles 4.5 cm. long and blades 12.5 x 6.3 cm. in size. He reported it from the Clarence River in northeast New South Wales. Domin also mentions a narrow-leaved form, *stenophylla* from south Queensland. Its leaves measure 10-11 x 3 cm., and 14-17 x 5.5 cm. It is not the intention of this paper to divide *F. macrophylla* into forms and it seems likely that such may be temporary results of cultivation of a variable species under different external conditions. Guilfoyle (Australian plants 178. 1911) speaks of a golden-leaved Moreton Bay fig tree of garden origin.

Summary

Ficus macrophylla Desf. ex Pers., a native of Australia, is used in Florida as a shade, roadside and specimen tree. It may be killed to the ground by a heavy frost, but had been found to renew its above-ground structure.

The tree is recognized by its large, ovate or elliptical, shining leaf blades, which taper to the apex and are borne on petioles almost as long as the blade is wide. The fruit is round and pedunculate, and, according to Nehrling, does not seed, perhaps because it lacks the proper kind of insect to pollinate it.

At least eight synonyms are listed, but no varieties seem valid. Several forms, based on leaf size or color variation, have been reported.

Illustrations of parts of *F. macrophylla* may be found in Bailey (above, *pl. 483.* 1913), Francis (Australian rain-forest trees, *pl. 31, 32.* 1929), Mowry (above, *pl. 41.* 1938), Barrett (Leaf key Florida trees, *pl. 4, f. 5.* 1937).

Living specimens often have been planted in Florida.

Ficus lacor var. cunninghamii

For about 75 years this fig tree has been known as *Urostigma cunninghamii* or *Ficus cunninghamii,* although its relation to *F. lacor* (previously called *F. infectoria* Roxb.) occasionally was suspected. In 1921 Domin declared it a variety of *F. infectoria.* The combination *F. lacor* var. *cunninghamii* is

new, so far as I know. The discussion of the following synonymy will employ correct spelling of the titles cited, but will sometimes use *"F. infectoria"* if that name is given by other writers. It will include also the relation of var. *cunninghamii* to *F. lacor* var. *typica* and to *F. lacor* var. *lambertiana.*

Ficus lacor Ham. Trans. Linn. Soc. **15**: 150. 1827 var. **cunninghamii** (Miq.) Barrett, comb. nov.

Urostigma cunninghamii Miq. Hook. Lond. Journ. Bot. **6**:560. 1847. *U. fraseri* Miq. (above) **6**:561. *U. psychotriifolium* Miq. (above) **6**:561. *F. cunninghamii* (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. **3**:286. 1867. *F. psychotriifolia* (Miq.) Miq. Ann. (above) **3**:286. *F. caulobotrya* (Miq.) Miq. var. *fraseri* (Miq. 1847) Miq. Ann. (above) **3**:287. *F. fraseri* (Miq. 1847) Muell. Fragm. Phyt. Australiae **6**:195. 1868 (not *F. fraseri* Miq. 1848). *F. syringifolia* C. Fraser ex C. Moore, Handb. New South Wales 81. 1893 (not *F. syringifolia* Kunth & Bouché). *F. infectoria* Roxb. var. *cunninghamii* (Miq.) Domin, Bibl. Bot. **89**:562. 1921. *F. infectoria* Roxb. var. *fraseri* (Miq. 1847) Domin (above). *F. infectoria* Roxb. var. *psychotriifolia* (Miq.) Domin (above).

Evergreen or sometimes deciduous glabrous tree; in Australia small or to 25 m. high, trunk divided near base, sometimes formed by aerial epiphytic roots which may increase its diameter to 12 m. and give it a deeply grooved appearance, buttress roots occasionally 6 m. long, branches spreading to 30 m. and sometimes with aerial roots reaching ground; in Florida a smaller tree with light-colored, slightly furrowed bark marked with horizontal lenticels; stipules of terminal buds ovate, 6 mm. to 5 cm. long, acute, often rosy or deep pink, elongating and partly deciduous; petioles 2.5-6.5 cm. long; blades leathery but not thick, mostly decidedly oblong, the largest 12-16 x 5.5-7.5 cm.; apex rounded, then abruptly narrowed into a slender oblong tip to about 1 cm. long; base usually rounded but occasionally truncate, subcordate or slightly narrowed; margin entire; upper surface shining; midrib prominent, bearing a gland on under surface above petiole; basal veins of same thickness as secondary lateral veins, but at a slightly more acute angle; 7-12 sets of secondary lateral veins, distinct, but not much raised, upper midrib angle 45°-50°, forking and uniting to form a deeply indented inframarginal vein; the place of a tertiary vein taken by a zigzag boundary of sections of the reticulum; no checkered background; figs paired at first, axillary, sessile, globose, 8-10 cm. in diameter, glabrous, whitish to purple or rose-tinted, sometimes spotted, yellowish when dry; ostiole not prominent; three small basal bracts concealed by the base of the fig; male flowers reported to be few, located under apical bracts, perianth stipitate with three parts, stamen shorter than perianth; female flowers more numerous, more or less sessile, stigma acute, filiform, slightly dilated towards base.

TYPE: dense woods, Brisbane River, Queensland. *A. Cunningham, collector.*
Distribution: Australia: Queensland, New South Wales.
Common Names: Cunningham's Fig. Queensland Fig.

Synonyms and Related Varieties

With the exception of *F. syringifolia* Fraser, which Moore listed without comment, the synonymy of var. *cunninghamii* is concerned only with that and

two other forms and with their relation to the type of the species and another variety. *U. fraseri* and *U. "psychotriaefolium,"* as Miquel spelled it, like *U. cunninghamii* were specimens in the herbarium of W. J. Hooker. *U. fraseri* had been collected by Fraser at Bremer River in southern New South Wales, and *U. psychotriifolium* by Fraser at the Brisbane River in south Queensland.

Miquel's description of *U. "cunninghami"* brought out the principal distinguishing characters to be found in its dried specimens. Later writers, such as Bentham (Fl. Australiensis 6: 165. 1873), Mueller (Fragm. Phyt. Australiae 8: 246. 1874, and Sel. Extr. Pl. ed. 9: 226. 1895) and F. M. Bailey (Queensland Fl. 5: 1468. 1902) could add little except habit characters from living trees and slightly extended dimensions of organs.

Miquel's characterization of *U. fraseri* differed from his of *U. cunninghamii* in the shorter, but relatively wider elliptical or obovate-elliptical leaf blades, with a longer tip and a narrower base. No figs were reported, and Bentham (above) declared that the species was founded upon a specimen in leaf only.

U. psychotriifolium had leaves of the same shape as those of *U. fraseri,* but a little smaller. The apex was obtusely apiculate and the base apparently more narrowed than in that species. The receptacle was described as smaller than a cherry and very short-peduncled. Bentham (above) claimed that Miquel made this species from a single specimen with one damaged receptacle.

When Miquel transferred *U. cunninghamii* and *U. psychotriifolium* to *Ficus,* of which *Urostigma* now is considered a sub-genus, he could not do the same for *U. fraseri* because he had previously (Hook. Lond. Journ. Bot. 7: 235. 1848) given the name *Ficus fraseri* to a rough- and sometimes lobed -leaved species. He therefore made *U. fraseri* a variety of *F. caulobotrya,* which as *U. caulobotryum* he had described from the "East Indies." This was a form with fascicled, pedunculate receptacles. Mueller in June 1868 had transferred Miquel's *U. fraseri* to *Ficus;* but, of course, was preceded by that author's *F. fraseri* of 1848.

Mueller, in speaking of his own *F. fraseri,* had pointed out that the three Australian species of *Urostigma* seemed closely related; and Bentham (above) had remarked that some forms of *F. cunninghamii* were like those of the other two. Maiden (Usef. Pl. Australia 537. 1889) and Bailey (above) cited the three species of *Urostigma, F. fraseri* (Miq.) Muell. and *F. psychotriifolia* as synonyms of *F. cunninghamii.* Domin (above) believed all three to be distinct varieties of *F. infectoria* Roxb.

F. infectoria Roxb. is the old and erroneous name for *F. lacor* Ham. Roxburgh applied this specific title to a well-known Indian tree, incorrectly believing that it was the same plant which Willdenow had called *F. infectoria.* But *F. infectoria* Willd. previously had been named *F. tsjahela* Burm. f. (misspelled *tsjakela,* see Barrett, Bull. Torrey Club 73: 86. 1946.) so that the title *infectoria* was invalidated and should not have been used again in connection with *Ficus.* Nevertheless, *"F. infectoria"* with Roxburgh as author continued to be applied to the Indian tree. There has been some question as to the identity of *F. lacor* Ham. with Roxburgh's species, but Hamilton's name

has been accepted by such authorities as Schneider (*in* Sargent, ed. Pl. Wilsonianae 3[2]: 309-310. 1916), Handel-Mazzetti (Symb. Sin. 7: 92-93. 1929) and Rehder (Journ. Arnold Arb. 10: 124. 1929).

Bentham (above) declared that *F. cunninghamii* was too close to *F. infectoria* Roxb., differing slightly in leaf shape and acumen. King (Ann. Bot. Gard. Calcutta 1: 50. 1887) stated that all the sheets of *F. cunninghamii* in the Kew collection belonged to *F. infectoria,* and most of them to its variety *lambertiana;* but he did not allocate *cunninghamii* definitely to that species. F. M. Bailey (Compr. Cat. Queensland Pl. 486. [1913]) made *F. cunninghamii* a synonym of *F. infectoria;* and Domin, as has been said, announced it as a variety of that species. Francis (Australian Rain-for. Trees 64. 1929) has said that fresh specimens of *F. cunninghamii* from south Queensland seemed to differ from King's description and figures of *F. infectoria* only in the larger size of the receptacle of the former plant, but that King's material may have been dry. Since specimens in the Queensland Herbarium agreed with the typical form of *F. infectoria* he adopted that as the name of the Australian tree. However, the leaves which Francis showed (*pl. 27*) as an illustration of *F. infectoria* are more like those of its variety *lambertiana,* as are also the pitted, although sessile receptacles.

These confusing relationships have been well summarized by Koorders, as quoted in Koorders & Valeton, Booms. Java 11: 139. 1906. He said that the most extreme forms of *F. infectoria* in his herbarium corresponded with the four varieties (Indo-Malayan and Chinese) separated by King (above, pp. 62-63), but that almost all the forms ran into one another. Although *cunninghamii* was not mentioned in this statement, since it is not native to Java, its inclusion seems logical.

At first sight the high-shouldered oblong leaf of *cunninghamii* appears very different from the more ovate and gradually tapering one of *F. lacor.* However, an examination of a tree labeled *F. infectoria,* in the Royal Palm Nurseries, Oneco, Florida, showed leaves of the type of the species predominating, but also some which resembled blades of *cunninghamii,* and were like specimens from the Queensland Herbarium, *no. 6907, F. cunninghamii,* collected by C. T. White. The Oneco tree, according to the catalog of the Nurseries, came from India. It is a typical specimen of what should be called *Ficus lacor* Hamilton, Trans. Linn. Soc. 15: 150. 1827. var. *typica* (Domin, Bibl. Bot. 89: 563. 1921) Barrett, comb. nov. (*Ficus infectoria* var. *typica* Domin). Although the herbarium of the New York Botanical Garden contains several specimens from Australia labeled *F. infectoria* none seems to me to belong to var. *typica;* and, indeed, C. T. White, who collected three of them, has said (Contrib. Arnold Arb. 4: 18. 1933) that he did not try "to place them varietally." Most of his resemble var. *lambertiana* as to leaves and figs.

Ficus lacor Hamilton, Trans. Linn. Soc. 15: 150. 1827 var. *lambertiana* (Miquel, *in* Hooker, London Jour. Bot. 6: 565. 1847) Barrett, comb. nov. (*Urostigma lambertianum* Miquel) has not been seen by me in Florida, nor has it been reported from that state so far as I know. But F. M. Bailey (Compr. Cat. Queensland Pl. 486. [1913]) said that it was a common Queensland form, Domin (above, p. 562) reported it from Australia, King (above)

inferred the same, Francis (above) and Brandis (Indian trees *pl. 186.* 1906) illustrated it as *F. infectoria* and specimen *no. 10184* of the Queensland Herbarium, collected at Haymen Island, is typical of that variety.

Lambertiana differs from other forms of the species in its large ovate leaf blades with a broad base and a gradually tapering and then abruptly acuminate apex. Typical figs are larger than those of vars. *typica* and *cunninghamii,* and sometimes when dry are pebbly surfaced. They are more or less pedunculate. Parts except the leaves occasionally are hairy. This variety is not likely to be confused with var. *cunninghamii.*

Summary

The Australian tree long known as *F. cunninghamii* (Miq.) has been determined as *F. lacor* Ham. var. *cunninghamii* (Miq.) Barrett, comb. nov. Two other forms of *Ficus,* originally named by Miquel, *fraseri* and *psychotriifolia,* as well as *F. syringifolia* Fraser ex Moore are synonyms.

The new combinations of this and varieties *typica* and *lambertiana* result from the modern acceptance of *lacor* as the name of the species, instead of *infectoria* Roxb., a title given by Roxburgh to a new species which he incorrectly supposed was *F. infectoria* Willd., and retained after Willdenow's name was invalidated.

Cunninghamii is variable, but in its most typical forms has a distinctive oblong, high-shouldered leaf with a generally rounded or truncate base and a rounded, and then abruptly acuminate apex. The tip is noticeably slender. The whitish figs are about 1 cm. in diameter, are marked with a pinkish tinge and are sessile. Specimens were seen on the estate in Miami of Mrs. C. T. Simpson, and in Bay Front Park, Miami, labeled *F. lacor.*

From *cunninghamii* var. *typica* differs in its slender ovate leaves with a more gradually tapering tip. Full grown trees are apt to have composite trunks. The figs are like those of var. *cunninghamii. Typica* is extremely variable as to leaves, and may approach *cunninghamii* in one direction and var. *lambertiana* in the other. I have seen no typical Australian specimens of this variety.

Var. *lambertiana* is comparatively stable and is recognized by its rather large, broad ovate, almost triangular leaves and its sometimes pedunculate pebbly or hairy figs, more than 1 cm. in diameter. This is an Australian form, but it is not reported from Florida. Like var. *typica* it was first described from India, in contrast to var. *cunninghamii,* which seems to be confined to Australia in its native distribution.

Ficus platypoda var. petiolaris

Miquel (Hook. Lond. Jour. Bot. 6: 561-562. 1847) described some Australian specimens of fig trees in Hooker's herbarium as *Urostigma platypodum.* The specific name referred to their broad, flat, leaf petioles, and was derived from *Ficus platypoda,* a title given by A. Cunningham in manuscript to those of the above specimens which he had collected at York Sound in northwestern Australia. *Urostigma* no longer exists except as a sub-species *of Ficus;* so Cunningham's name, poorly quoted by Miquel in 1867, has become valid.

The original mention of it, in 1847, was merely the citation of *F. platypoda* Cunn. MS. as a synonym.

Hooker's herbarium specimens of *U. platypodum* were divided by Miquel into three forms: those of Cuningham, later called forma *elliptica* by Miquel (Journ. Bot. Néer. 1: 236. 1861); forma *minor glabrior* from northwestern Australia, later (1861) entitled forma *glabrior;* and a larger set collected by Fraser in southern Queensland and northwestern New South Wales. This Miquel (1861) named forma *major*. Forma *elliptica, according* to the stated locality, was the type of the species, and has been called var. *typica* by Domin (Bibl. Bot. 89: 564. 1921); forma *minor glabrior* is var. *minor* (Miq.) Benth. Fl. Australiensis 6: 169. 1873; and forma *major* has become var. *petiolaris* Benth. These changes of name are in accordance with article 58 of the International Rules of Botanical Nomenclature.

Petiolaris seems to be the best known of the varieties of *F. platypoda*. In Florida it has been cultivated at Chapman Field. It has been tentatively suggested for southern Florida by G. R. Wilson (Proc. Florida Hort. Soc. 1937: 66. 1938).

FICUS PLATYPODA A. Cunningham ex Miquel, Ann. Mus. Bot. Ludg. -Bat. 3: 287. 1867 var. PETIOLARIS Bentham. Fl. Australiensis 6: 169. 1873.

Urostigma platypodum forma *major* Miq. Journ. Bot. Néer. 1:236. 1861.

A glabrous tree reported to become 16 m. tall in Australia; branches bearing aerial roots; twigs pale, brownish; stipules of terminal buds long, narrow; leaf petioles rather broad, usually 3-5 cm. or more in length; blades elliptical, 9-14 x 4-7.5 cm. (examples: 10 x 5, 11.5 x 5, 14 x 7 cm.); apex obtuse or very short acuminate; base rounded or wide cuneate; upper surface shining dark green, lower surface bluish-green, both surfaces becoming light-colored when dry; two basal veins making an angle of about 90°, of about the same thickness as the secondary lateral veins, 12-18 sets of slender parallel secondary veins, upper angle at midrib about 60°, forking and uniting to form an inframarginal vein; one continuous tertiary vein between consecutive secondaries, almost equaling their thickness; reticulum faint, especially the cross partitions; checkered background distinct under a lens; figs axillary, originally paired, globose, glabrous but warty, bright deep yellow, about 1 cm. in diameter; apex slightly umbonate because of apical bracts; basal bracts deciduous, leaving a disk; peduncle 2-5 mm. long.

TYPE: Brisbane and Hastings Rivers, Queensland and New South Wales, Australia. *Fraser, collector.*

Distribution: Queensland and New South Wales, Australia.

Common Name: Small-leaved Moreton Bay Fig.

Commentary

The type locations of Fraser's specimens were originally stated by Miquel as Brisbane and Hastings River; but Bentham (above) believed that the Brisbane River was meant.

Bentham (above, p. 170) described also varieties *mollis* and *subacuminata*

from Queensland, but placed an interrogation point before their specific names, as he had done before *petiolaris*. The reason for this indecision is seen in his remark that the first two varieties were Miquel's *F. leichhardtii*, according to F. von Mueller's herbarium; but that the type specimens of that species were not in Mueller's collection, unless they were the ones cited from the type location of *F. leichhardtii*, but placed under *petiolaris*. If the three varieties were the same species, that should be called *F. leichhardtii*, he declared.

So far as *petiolaris* is concerned it appears to be quite distinct from *F. leichhardtii*, which was a variable-leaved hairy form described as *Urostigma* by Miquel in 1861, from Cleveland Promontory in northeastern Queensland. Var. *mollis*, however, agrees well with *F. leichhardtii;* and var. *subacuminata* apparently accords with var. *angustata* of that species. If they prove to be the same, Bentham's name *subacuminata* would be changed to *F. platypoda* var. *angustata* (Miq.) Benth. However, F. M. Bailey (Queensland Fl. 5: 1466. 1902) has described Bentham's three varieties in the words of their author, and also has illustrated them (Compr. Cat. Queensland Pl. *pl. 479-481.* [1913]). Var. *mollis* is mentioned also by C. T. White (Contrib. Arnold Arb. 4: 19. 1933) and specimens so determined by him are in that herbarium. *Mollis* resembles *petiolaris* closely, except for its general hairiness.

Summary

Ficus platypoda A. Cunn. ex. Miq. var. *petiolaris* Benth. is a distinct variety of the species and has been grown in Florida. It is native to Queensland and New South Wales, Australia.

Its elliptical, long-petioled leaf somewhat resembles those of some other Australian species or varieties, but may be distinguished as follows: from *F. macrophylla* and *F. watkinsiana* by its smaller size, from *F. lacor* var. *cunninghamii* by its less oblong shape and less acuminate apex, and from *F. henneana* by its basal veins, less distinct reticulum and checkered background. Its globose yellow fig on a short peduncle differs in color from those of the other forms just mentioned, is not sessile like that of *F. lacor* var. *cunninghamii*, and is much smaller than those of the other species.

Specimens have been studied outdoors in Florida and in herbaria. All agreed well with each other and with the descriptions and illustrations mentioned in the text.

Ficus henneana

Ficus henneana was growing at Chapman Field, in 1937. At that time it was a small tree with epiphytic roots which enlarged the diameter of the stem to 2 dm. at the base, and also served as props. Other specimens may have been distributed through the state, although they have been reported seldom, if at all. The species has been seen also in the herbarium of the Arnold Arboretum.

FICUS HENNEANA Miq. Ann. Mus. Bot. Ludg. -Bat. 3: 216. 1867.

Glabrous shrub or tree reported to reach a height of about 9 m. in Australia; trunk slender, or large if formed by epiphytic roots; prop roots and

roots from branches often present; branches few, stout, horizontal; twigs slender, erect, dark gray; stipules covering a short, green, conical terminal bud; petioles mostly about 2.5 cm. long, occasionally to 4 cm., slender; leaf blades thin but not papery, elliptical or very slightly obovate, the largest 9-12.5 x 4.5-7 cm. (examples: 10 x 5, 12 x 6.5 cm.); apex slightly narrowed, obtuse or gradually short- and obtuse-acuminate; base rounded or slightly narrowed or subcordate; margin entire, not flat when dried; upper surface shining dark green with a yellowish midrib; lower surface paler, dull, waxy, olive-green with reddish veins; basal veins not different from secondary lateral ones, of which there are 8-13 sets, upper angle 50°-70°; one irregular tertiary between each two consecutive secondary veins and forming with them a deeply indented inframarginal vein; reticulum better visible on upper surface, composed of many small irregular sections; no checkered background; figs axillary, paired at first, globose, usually about 2 cm. in diameter, smooth, red, spotted with white, turning to yellow when dry, slightly umbonate at the apex because of apical bracts; basal bracts soon deciduous, leaving disk; peduncle 2-7 mm. long; male flowers reported few, short-stipitate, with three perianth parts, and one stamen with a large anther and a very short filament; female flowers containing a subulate stigma.

TYPE: Booby Island, Torres Strait, northern Queensland, *Henne, collector.*

Distribution: Australia: Queensland, New South Wales, Northern Territory.

Common Name: Cedar Fig.

Comparison of F. henneana with Other Species

Domin (Bibl. Bot. 89: 566. 1921) has asserted that *F. henneana* should be called *F. muelleri* (Miq.) Miq. Ann. Mus. Bot. Ludg.-Bat. 3: 268. 1867, which, first described as *Urostigma muelleri* Miq. Journ. Néer. 1: 235. 1861, would antedate *F. henneana.* Domin declared that an example from Hastings River, New South Wales, *Beckler, collector,* was not different from *F. henneana.*

The type specimens used by Miquel for *U. muelleri* were Mueller's and came from the Hastings River region. The collector was not named by Miquel, but may have been Rudder, for Mueller (Fragm. 8: 246. 1874) mentioned that person as the author of a note on the habit of *F. muelleri.* Miquel (Ann. above, p. 268) referred to *F. nesophila* (Miq.) Muell. some specimens of Beckler's from Hastings River, but did not connect them with *F. muelleri.* Bentham (Fl. Australiensis 6: 167. 1873) listed Beckler's plant under *F. muelleri,* and made no reference to other material from that collector in his description of *F. nesophila* (above, pp. 164-165).

A comparison of Miquel's original characterizations of the two species fails to bring out many differences. The only apparent ones are: the leaf blades, which Miquel said measured 8.75-12.5 x 9.5-7.5 cm. in *F. henneana* and 10-17.5 x 5-6.5 cm. in *F. muelleri;* the glabrous surface of the former plant as contrasted with pubescence in some parts of the latter; a wavy blade margin versus an inrolled one; deciduous basal bracts instead of (apparently)

permanent ones; and the location of *F. henneana* on an ocean island at about 10° south latitude, and of *F. muelleri* near 30.5° south latitude.

None of these distinctions is very valuable except perhaps that concerning the basal bracts. The lower limit of the blades' width in *F. henneana* obviously is a misprint, and the upper limit of the blade's length in *F. muelleri* is too great, according to reports by other writers. The character of pubescence in *F. muelleri* was changed to glabrous by Bentham, although Miquel (Ann. 3: 268) again implied it by intimating that the species might be confused with *F. leichhardtii*, which he had described as hairy. The appearance of leaf margins in herbarium specimens sometimes is affected by the pressing.

Nevertheless, some other differences between *F. henneana* and *F. muelleri* have been brought out, principally by Bentham (above, pp. 165-166) and F. M. Bailey (Compr. Cat. Queensland Pl. *pl. 482.* [1913]). From these it appears that *F. muelleri* is a very tall tree; with leaf petioles usually not more than 3 cm. long, sometimes obovate blades not more than 10 cm. in length and with a generally narrowed base, figs not larger than 1.5 cm. in diameter, and stamens taller than the male perianth. I have seen no specimens of *F. muelleri*, but believe that these reports differentiate it from *F. henneana*.

Resemblances between *F. henneana* and *F. nesophila* have been commented on by Miquel (Ann. 3: 216), Bentham (above, pp. 165-166) and others. The latter is a perplexing form originally described by Miquel (Journ. Bot. Néer. 1: 237. 1861) as *Urostigma nesophilum*. He used incomplete specimens in Mueller's herbarium, obtained on Quail Island in Northern Territory by an unnamed collector.

F. nesophila evidently bears some resemblance to *F. henneana*, but differs from it in its smaller figs on shorter peduncles. It has been thought to be a form of *F. lacor* Ham. (previously known also as *F. infectoria* Roxb.), but has been allocated as a variety to *F. glabella* Blume by King (Ann. Bot. Gard. Calcutta 1: 50. 1887), F. M. Bailey (above, p. 485), Domin (above, p. 561), and others.

Summary

F. henneana Miq. is a possibility for cultivation in southern Florida. Although its leaves and figs somewhat resemble those of *F. muelleri*, *F. lacor* var. *cunninghamii*, *F. platypoda* var. *petiolaris*, and *F. glabella* var. *papuana* it may be distinguished by its elliptical leaf blades, with a short thick acumen and a rounded base without distinct basal veins; and by its figs, which measure 2 cm. in diameter, and possess peduncles several mm. in length and deciduous basal bracts.

Small leaves from a tree at Chapman Field agreed with those shown by F. M. Bailey (Compr. Cat. Queensland Pl. *pl. 472.* [1913]). Figs there pictured were like those of the specimen in the Arnold Arboretum.

MONTCLAIR, NEW JERSEY.

Development of Prairie at Iowa Lakeside Laboratory

W. A. Anderson

In 1930 the Iowa Lakeside Laboratory came into possession of a tract of prairie land lying in Section 23, T. 99 N., R. 37 W., Dickinson County, Iowa, and adjoining the original Lakeside Laboratory property on Miller's Bay, West Lake Okoboji. Previous to its purchase the tract had been grazed heavily but is said never to have been plowed. Since its purchase the tract has been kept free from grazing with the hope that prairie would be renewed on it. It is thus the basis for an experiment in plant succession, not in a perfectly natural state, but as near such as present conditions in Iowa permit. The writer made a preliminary report on this project in 1936 (1).

Dickinson County, Iowa, is in the northwestern part of the state, well within the region of "true prairie" as defined by Weaver and Fitzpatrick, (9) and Weaver and Clements (8). The Lakeside Laboratory tract of approximately 60 acres lies in the western moraine of the Wisconsin drift and is typical of the rougher ground of northwestern Iowa. (See plates 1 and 2.) It rises from lake level to about ninety feet above lake level (approximately 1400 to 1500 feet above sea level). Its general slope is to the southeast. Three systems of shallow ravines lead to the lake and two of these have permanent springs in them. Even at higher level than these springs there are undrained pockets, of the sort found in moraines everywhere, which contain water in

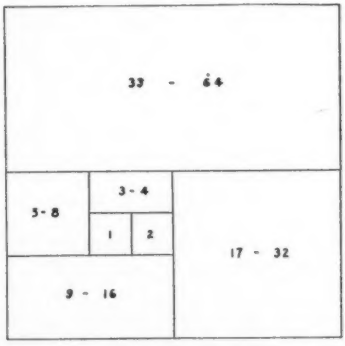

Diagram of laying out square meters

rainy periods. In 1945 the appearance of sedge meadow in several such places where hitherto only blue grass, red top and timothy had grown, lends color to the suspicion that all these ravines once supported hillside fen floras (2).

Certain quadrats had been the subject of study previous to 1935. A suitable size had been determined at 3 meters on a side (9 sq. m.). The suit-

ability of this sized quadrat has been tested a number of times in succeeding years. The method used is as follows.

A meter square is marked out with tape and species list made.

An adjoining square meter is laid off and all species not in the first sample are listed. This plot is then doubled and redoubled until 16, 32 or 64 square meters have been examined, with list of additional species made for each increase in size. (See diagram, Page .) The relation of species to area is plot-

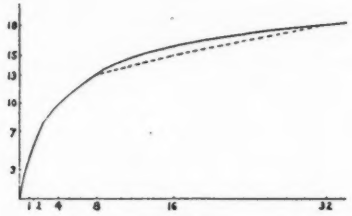

FIGURE 1

I Size of sample, north of Laboratory tract

1st square meter—*Poa pratensis, Aster laevis, Ambrosia artemisiaefolia.*
2nd square meter, add—*Solidago canadensis, Verbena stricta, Asclepias syriaca, Aster ericoides.*
3rd-4th square meter, add—*Solidago rigida, Bouteloua curtipendula, Tragopogon pratensis.*
5th-8th square meter, add—*Asclepias verticillata, Viola pedatifida, Andropogon furcatus.*
9th-16th square meter, add—*Melilotus officinalis, Lactuca canadensis.*
17th-32nd square meter, add—*Cirsium canescens, Melilotus alba, Phleum pratense.*

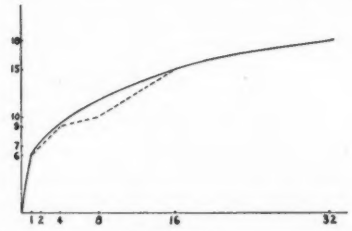

FIGURE 2

II Size of sample, north part of tract

1st square meter—*Poa pratensis, Andropogon furcatus, Aster ericoides, Ambrosia artemisiaefolia, Bouteloua curtipendula, Viola pedatifida.*
2nd square meter, add—*Phleum pratense.*
3rd-4th square meter, add—*Trifolium repens, Andropogon scoparius.*
5th-8th square meter, add—*Asclepias syriaca.*
9th-16th square meter, add—*Kuhnia eupatorioides, Melilotus alba, Agropyron subsecundum, Tragopogon pratensis, Physalis heterophylla.*
17-32nd square meter, add—*Aster laevis, Solidago rigida, Anemone cylindrica.*

ted as a curve with area on the horizontal axis and number of species on the vertical. These curves invariably take the form of the ones accompanying. Minimal area is indicated where the slope of the curve decreases abruptly.

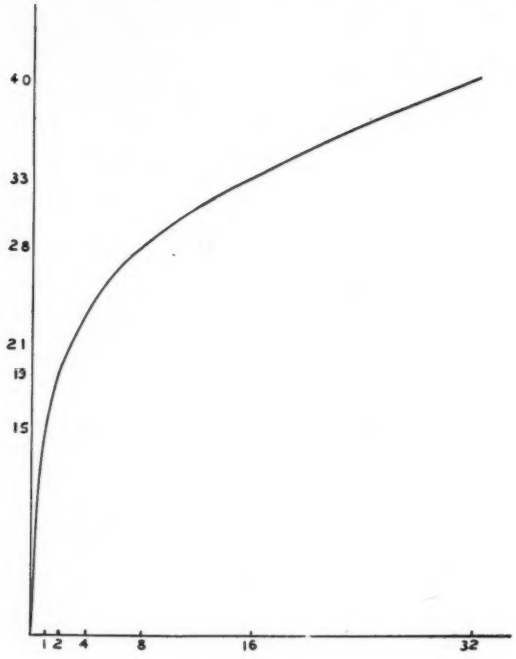

FIGURE 3

III Size of sample, prairie at south of section

1st square meter—*Andropogon scoparius, Andropogon furcatus, Petalostemum candidum, Helianthus rigidus, Agropyron subsecundum, Petalostemum purpureum, Amorpha canescens, Phlox pilosa, Anemone patens,* var. *Wolfgangiana, Antennaria* sp. *Panicum Scribnerianum, Lithospermum incisum, Bouteloua curtipendula, Poa pratensis, Liatris scariosa.*

2nd square meter, add—*Coreopsis palmata, Aster laevis, Lobelia spicata, Pedicularis canadensis.*

3rd-4th square meter, add—*Allium stellatum, Silphium laciniatum.*

5th-8th square meter, add—*Polygala verticillata, Equisetum laevigatum, Melilotus alba, Solidago rigida, S. glaberrima, Anemone virginiana, Erigeron ramosus.*

9th-16 square meter, add—*Solidago speciosa, Elymus canadensis, Koeleria cristata, Phleum pratense, Aster sericeus.*

17th-32nd square meter, add—*Brauneria angustifolia, Sorghastrum nutans, Astragalus canadensis, Rosa suffulta, Lathyrus palustris, Stipa spartea, Agrostis hyemalis.*

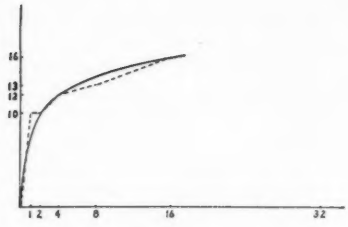

FIGURE 4

IV Size of sample, high ridge, center of tract

1st square meter—*Poa pratensis, Andropogon furcatus, A. scoparius, Bouteloua curtipendula, Viola pedatifida, Cirsium canescens, Asclepias syriaca, Lithospermum incisum, Ambrosia artemisiaefolia, Aster ericoides.*

2nd square meter, add—None.

3rd and 4th square meter, add—*Tragopogon pratensis, Sporobolus heterolepis.*

5th-8th square meter, add—*Amorpha canescens.*

9th-16th square meter, add—*Petalostemum purpureum, Solidago rigida, Physalis heterophylla.*

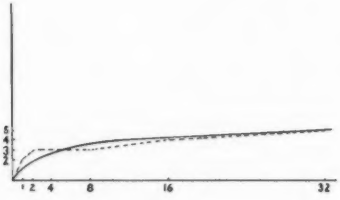

FIGURE 5

V Size of sample, blue grass, south part of tract

1st square meter—*Poa pratensis, Physalis heterophylla.*

2nd square meter, add—*Ambrosia artemisiaefolia.*

3rd, 4th square meter, add—None.

5th-8th square meter, add—None.

9th-16th square meter, add—*Asclepias syriaca.*

17th-32nd square meter, add—*Phleum pratense.*

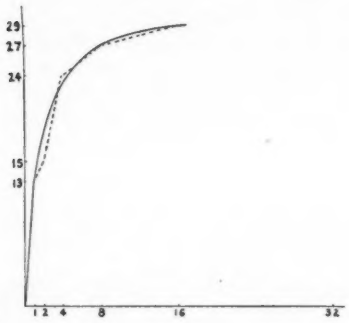

FIGURE 6

VI Size of sample — Lookout Knob, 1938

1st square meter—*Helianthus rigidus, Coreopsis palmata, Aster ericoides, Panicum Scribnerianum, Poa pratensis, Elymus canadensis* var. *robustus, Agropyron subsecundum, Aster laevis, Viola pedatifida, Cirsium canescens, Andropogon scoparius, A. furcatus, Amorpha canescens.*

2nd square meter, add—*Solidago rigida, S. glaberrima.*

3rd-4th square meter, add—*Petalostemum candidum, Physalis* sp., *Phlox pilosa, Lactuca canadensis, Oenothera biennis, Commandra umbellata, Allium stellatum, Anemone cylindrica, A. patens,* var. *Wolfgangiana.*

5th-8th square meter, add—*Eryngium yuccaefolium, Phleum pratense, Stipa spartea.*

9th-16th square meter, add—*Aster sericeus, Brauneria angustifolia.*

These results indicate that a smaller sample than nine square meters would be satisfactory for either blue grass pasture or for well developed prairie, but that on the Iowa Lakeside Laboratory tract eight square meters is the smallest area which may be considered a representative sample. The square, 3 meters on a side, is not substantially different from this, and for consistent results, was employed on all prairies studied.

As to identification of plants on these prairies, the attempt has been made to keep up with modern ideas of classification. Since many data depend on field identification this has not always been carried to subspecific rank. Deam's excellent Flora of Indiana and Hitchcock's Manual of Grasses of the United States have been of great assistance in identifications.

Records of sixteen permanent quadrats have been kept from 1935 until the present, with the exception of 1943. The plants in these quadrats are estimated as to cover value and number according to a six-point scale.

x = sparsely or very sparsely present; cover very small
1 = plentiful but of small cover value
2 = very numerous, or covering at least 1/20 of area
3 = any number of individuals covering 1/4 to 1/2 of the area
4 = any number of individuals covering 1/2 to 3/4 of the area
5 = covering more than 3/4 of the area

This scale permits the consideration of both large and small plants at the same time. Estimates are made on foliage rather than stems. In this tract the growth is quite dense, giving total coverage. There is a small amount of layering, but with the exception of blue grass (*Poa pratensis*) the lowest layer has practically no cover value. In many places the blue grass sward is the only layer present.

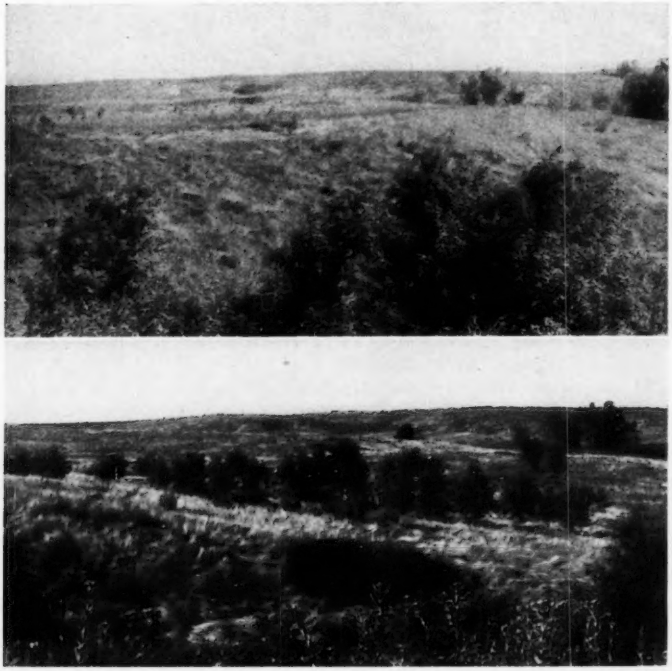

PLATE 1.—Iowa Lakeside Laboratory Prairie. General View—looking north from Cottage area. Top—August 1941. Bottom—August 16, 1945.

Estimates of cover value and number have been made each year without reference to plant lists or notes of previous years which might be prejudicial. Care has been exercised to recover the exact plot each year and to find all species apparent at the time of the visit.

The use of a scale of classes rather than actual percentages is justified by the fact that the getting of actual percentage is a difficult problem. It is rela-

tively easy to say that a given species covers 1/4, 2/4, 3/4, or 4/4 of the area. This estimate is sufficiently accurate to cover the more important changes in plant population and does not require an excessive amount of time. "All too often the attempts to combine the most exact counts and measurements of sample communities (stands) into an abstract unit (a plant association) results in nothing but vague averages. 'Measure what can be measured and count

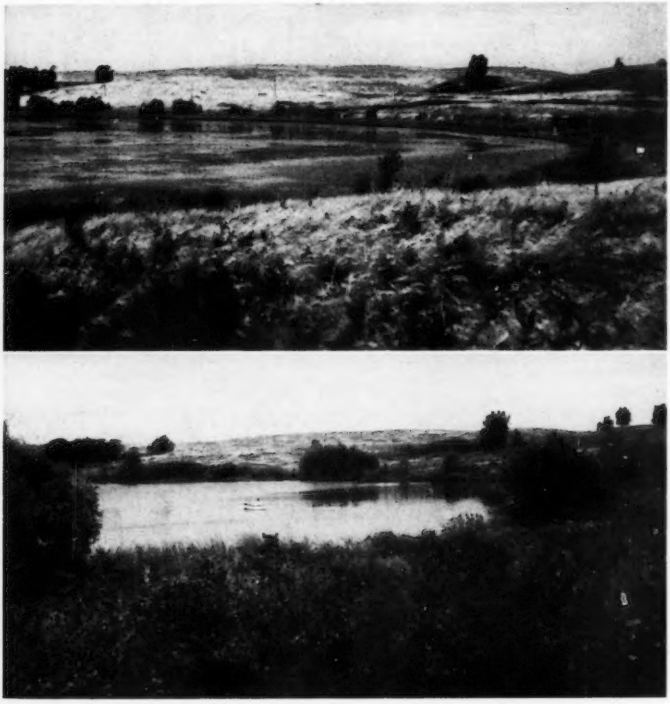

PLATE 2.—General View of prairie from across Little Millers Bay. top—July 31, 1935. Bottom—August 21, 1944.

what can be counted, but always be conscious that the figures obtained are purely relative.' Not infrequently mere estimation gives better results than counting and measuring." Braun-Blanquet, Fuller and Conard translation, p. 26 (3).

The following tables give yearly records of the presence and cover-grades of species on 17 permanent quadrats.

QUADRAT A_4

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	4	4	5	5	5	4	4	5	5	4
Ambrosia trifida	1	1	1	×	×	×	1		×	
A. artemisiaefolia	1	1	1	×		×	1	×	×	×
Lactuca (scariola?)	×	×	×							
Verbena stricta	×		×	×	×		×	×	×	
Agropyron repens	×									
Quercus macrocarpa	×									
Agropyron Smithii		×	1	1	1	1	2	1	2	2
Melilotus alba			1	×	×		×	×	×	1
Physalis virginiana			×	×	×	×	×		×	×
Chenopodium album			×			×	×			
Cirsium seedling			×							
									5 ft.	7 ft.
Acer Negundo				×	×		×	×	×	×
Erigeron canadensis				×						
Agropyron subsecundum						×				
Tragopogon pratensis							×			
Asclepias syriaca									×	×

QUADRAT A_6

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	5	4	5	5	5	5	4	5	5
Ambrosia artemisiaefolia	2	×	3	2		×	1	2	×	×
Trifolium repens	1		×							
Taraxacum sp.	×						×			×
Ambrosia trifida			×				×			
Lactuca sp.			×							
Verbena stricta			×	×	×	×	×		×	×
Oxalis sp.			×							
Acer Negundo				×						
Erigeron canadensis				×						

QUADRAT A_8

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	5	5	5	5	5	5	5	5	5
Phleum pratense	×	×	×							
Ambrosia artemisiaefolia	×	×								
Taraxacum sp.	1		×							
Trifolium repens	×									

QUADRAT A_8—Continued

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Aster ericoides	×	×								
Tragopogon pratensis			×							×
Agropyron Smithii							×			
Convolvulus sepium									2	1(2)
Asclepias syriaca										×

QUADRAT B_0

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	4	4	5	5	5	4	5	5	5	5
Phleum pratense	2	1	1	×	×	×	×			
Taraxacum	1		×							
Melilotus alba	1	×								
Verbena stricta	×	×	×							
Aster ericoides	×	×	×	×			×	×		×
Ambrosia artemisiaefolia	×		×	×			×	×		
Agrostis alba	2	1	1	×	×	×				
Asclepias syriaca			×	×	×	×	1	1	*2	1
Agropyron subsecundum				×			×			
									6 ft.	8 ft.
Acer Negundo						×	×	×	×	×
Tragopogon pratensis							×			×
Ambrosia trifida									×	×
Helianthus grosseserratus									×	1

* Fruiting.

QUADRAT B_2

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	4	4	5	4	4	4	4	4	3	3
Andropogon furcatus	2	×	2	2	2	2	2	2	3	2
A scoparius	2	×	2	2	2	2	2	2	2	1
Bouteloua curtipendula	×	×	1	×						
Ambrosia artemisiaefolia	×		×	×		×		×		
Aster ericoides	×	1	1	2	1	1	1	1	2	1
Cirsium canescens	1	1	1	1	×	×	1	1	×	1
Trifolium repens	×									
Viola pedatifida	×				×					
Taraxacum sp.	×									
Agropyron repens	×									
Verbena stricta	×		×	×	×					
Agropyron Smithii		1	×	×			×		×	1
Kuhnia eupatorioides			×	×	×	×		×	×	1

QUADRAT B_2—Continued

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Agropyron subsecundum			×	×			×	×		
Tragopogon pratensis					×					
Asclepias verticillata									×	×
Setaria lutescens									×	
Asclepias syriaca										×

QUADRAT B_4

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	4	4	5	5	5	5	5	5	5	5
Solidago rigida	×	×						1		
Aster ericoides	×	2	2	1	1	2	1	1	2	1
Taraxacum sp.	×		2	×						
Cirsium canescens	×	×		×	×	×	×	×	×	1
Agropyron Smithii	1		×	1	1	×	1	×	1	1
Verbena stricta	×	×	×	×	×	×	×	×	×	×
Phleum pratense	×		×							
Euphorbia sp.			×							
Ambrosia artemisiaefolia				×			×		×	
Aster laevis				×						
Solidago canadensis						×	×		1	1
Convolvulus sepium									×	×

QUADRAT B_6

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	3	4	4	4	4	4	5	4	4	5
Aster ericoides	2	3	3	2	2	2	2	2	3	2
Andropogon furcatus	2	1	2	1	2	2	2	1	1	2
Cirsium canescens	1		×	×	×	×	×	×		
Ambrosia artimisiaefolia	1		1	1		×	1	×	×	
Taraxacum	×		×							
Viola pedatifida	×		×	×	×		×			
Phleum pratense	×									
Agropyron repens	×									
A. Smithii	×		×	×	×	×	1	×	×	1
A. subsecundum			×				×	×		
Setaria lutescens			×							
Agrostis alba			×							
Kuhnia eupatorioides				×	×	×	×	×	×	×
Vicia americana								×	×	×
Asclepias syriaca								×	1	×
Solidago canadensis									×	1

QUADRAT C_1

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	4			5	5	5	5	5	4	4
Melilotus alba	2			×			×		3	*3(4)
Aster ericoides	1									
Verbena stricta	×									
Taraxacum	×								×	
Ambrosia artemisiaefolia	×						×	×	1	
Allium stellatum				×	×				×	
Agropyron subsecundum					×	?×	×	×	×	
Setaria lutescens								×	×	
Tragopogon pratensis								×		
Kuhnia eupatorioides									×	

* Fruiting. White sweet clover 6 ft. high covers entire plot. Poa is ground cover.

QUADRAT C_3

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	4	5	5	5	5	5	4	5	5
Taraxacum	1									
Hordeum jubatum	×									
Phleum pratense	×		×							
Ambrosia artemisiaefolia	×	1	1	1	×		1	2	2	×
Verbena stricta		×								
Tragopogon pratensis								×		×
Asclepias syriaca									*×	×
Agropyron Smithii										×

* Young.

QUADRAT C_5

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	4	4	4	5	4	5	5	5	4	4
Andropogon furcatus	2	2	2	2	2	2	2	2	2	2
Phleum pratense	×		×	×		×	×			×
Hordeum jubatum	×									
Cirsium canescens	1	×	×	×	×				×	×
Ambrosia artemisiaefolia	1	1	2	1		×	×	×	1	1
Trifolium repens	×									
Viola pedatifida	×		×	×	×		×	×		×
Bouteloua curtipendula	×		1	×	2	×		2	1	×
Agrostis alba	×									
Lithospermum incisum	×									
Verbena stricta	×		×							
Andropogon scoparius		×		×	×	×	×(1)	×	×	1

QUADRAT C_5—Continued

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Euphorbia sp.			×							
Agropyron subsecundum			×	×		×	×			×
Agropyron Smithii				×			×			
Erigeron ramosus				×						
Tragopogon pratensis					×					
Aster puniceus var. *lucidulus*							×	×	1	2
Sorghastrum nutans									2	
Asclepias syriaca									×	×

QUADRAT C_7

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	5	5	5	5	5	5	5	5	5
Phleum pratense	2	×	1	1	×	×				
Taraxacum	×	×	1	×						
Ambrosia artemisiaefolia	×		×	×				×	×	×
Aster ericoides	×									
Cirsium		×	×	×						
Xanthium commune			×							
Trifolium repens			×							
Asclepias syriaca									*×	×

* Young.

QUADRAT C_9

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	3	3	4	3	4	4	3	4	4	3
Andropogon furcatus	3	3	3	3	3	3	3	3	3	3
Viola pedatifida	×		×	×	×			×		×
Cirsium canescens	1	2	×	×	×					
Bouteloua curtipendula	1		×							
Ambrosia artemisiaefolia	1	3	1	1		×	×	1	×	×
Phleum pratense			2	1	1		×			×
Agropyron subsecundum			×			×	×	×		
Lactuca canadense			×						×	
Verbena stricta			×	×	×	×	×			
Agropyron Smithii					×					
Asclepias syriaca								×	*1	1
Agropyron repens							×			

* Fruiting.

QUADRAT C_{11}

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	5	4	4	5	5	5	5	5	5
Andropogon furcatus	1	×		×	×	×	×	1	×	×
Ambrosia artemisiaefolia	1	×	3	1		×	1	1	1	1
Taraxacum	1		×	×						
Cirsium canescens	×		×	×						
Phleum pratense	1		×						×	×
Agropyron repens	×									
Koeleria cristata	×									
Bouteloua curtipendula	×		×	×	1	×		×	×	
Agropyron Smithii	×	×								
Verbena stricta		×	×	×	×	×	×	×		
Andropogon scoparius			×							
Agropyron subsecundum			×	×	×	×	1			×
Viola pedatifida				×			×			
Acerates viridiflora					×	×				
Petalostemum purpureum						×	×	×	×	×
Asclepias syriaca								×	*×	1
Oenothera biennis							×			
Aster ericoides									1	1

* Fruiting.

QUADRAT C_{13}

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	3	2	2	3	2	3	3	3	3	1
Andropogon scoparius	3	3	2	2	2	2	2	1	×	×
A. furcatus	2	2	2	2	3	2	4	3	3	4
Aster ericoides	1	1	×	1	1	1	1	1	×	1
Solidago rigida	1	1	2	×	1	×	2	2	2	2
Cirsium	1		×							
Verbena stricta	×	×	×	×	×		×	×		
Taraxacum	1	×	×							
Ambrosia artemisiaefolia	1	×	3	1		1	×			
Amorpha canescens	×	×	×	×	×	×	×	×	*1	×
Viola pedatifida	×		×			×	×		×	×
Solidago nemoralis	×		×							
Muhlenbergia cuspidata			2							
Bouteloua curtipendula			×	×	1			×	×	
Asclepias verticillata			×							
Linum sulcatum			×	×						
Erigeron annuus			×							
E. ramosus				×						
Acerates viridiflorus						×				
Asclepias syriaca							×		×	×
Lactuca canadensis										×

* Fruiting.

QUADRAT C_{15}

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	5	5	5	5	5	4	5	5	5
Agropyron Smithii	2	.....	1	1	1	1	2	1	1	1
Tragopogon pratensis	×	.....	.....	.....	.....	.....	.....	.....	.....	×
Equisetum laevigatum	×	.....	1	1	×	×	1	1	1	×
Verbena stricta	.....	×	.....	.....	.....	.....	.....	.....	.....	.....
Lactuca scariola	.....	.....	×	.....	.....	.....	.....	.....	.....	.....
Ambrosia artemisiaefolia	.....	.....	×	.....	.....	.....	.....	.....	.....	.....
Spartina pectinata	.....	.....	.....	×	2	1(?)	1	2	2	1

QUADRAT C_{17}

	1935	1936	1937	1938	1939	1940	1941	1942	1944	1945
Poa pratensis	5	5	5	.....	5	5	5	5	5	5
Tragopogon pratensis	×	.....	×	.....	.....	.....	.....	.....	.....	.....
Taraxacum sp.	×	.....	.....	.....	.....	.....	.....	.....	.....	.....
Verbena stricta	×	.....	.....	.....	.....	.....	.....	.....	.....	.....
Ambrosia artemisiaefolia	.....	.....	×	.....	.....	.....	.....	.....	.....	.....
Agropyron Smithii	.....	.....	.....	.....	.....	.....	.....	×	.....	.....
Cirsium canescens	.....	.....	.....	.....	.....	.....	1	1	.....	.....
Asclepias syriaca	.....	.....	.....	.....	.....	.....	.....	.....	×	×

Conclusions from Study of Permanent Quadrats

1. The record of these quadrats is evidence of the extreme stability of the plant cover and the slowness with which changes take place. Consider quadrat A_4. Of ten species found on it in 1937, five are still present in 1945, of nine species present in 1938, six are present in 1945 with addition of only one species.

Quadrat B_2 is more representative of prairie. Twelve species were found on it in 1935; in 1937 these had dropped to six, with one new species added for a total of seven. In 1945 six of these seven species are present and have been so in approximately the same proportions during the intervening years. Three additional species are now present; one, a prairie forb, has been there since 1937, the other two (milkweeds) are recent.

Quadrat C_{13} is on a knob in the midst of some of the most representative prairie on the entire tract. Out of twelve species listed in 1935 seven are present in 1945. In this case there has been an increase in Andropogon furcatus and Solidago rigida, with decrease in other species. Of five species which have disappeared, four are weeds.

In three quadrats, A_8, B_0 and C_{15}, there is invasion by spreading clones, respectively, Convolvulus sepium, Helianthus grosseserratus and Spartina pecti-

nata. In quadrat C_1 a profound disturbance was caused by a grass fire in the spring of 1944. This resulted in a dense growth of white sweet clover which in 1945 smothers everything else. This quadrat is on a knob surrounded by a fairly good growth of prairie, which seems unaffected by the fire. Other quadrats in the burned area seem affected not at all.

2. The study of these permanent quadrats must be made in reference to the seasons we have had, 1934 and 1936 were notably drought years, which culminated a series of dry years. In Dickinson County the drought ended with 1936; the seasons since have been reasonably moist. 1936 showed a marked decrease in number of species in all quadrats, mostly in weeds and introduced pasture plants, but also in a few prairie species. 1937 saw a corresponding

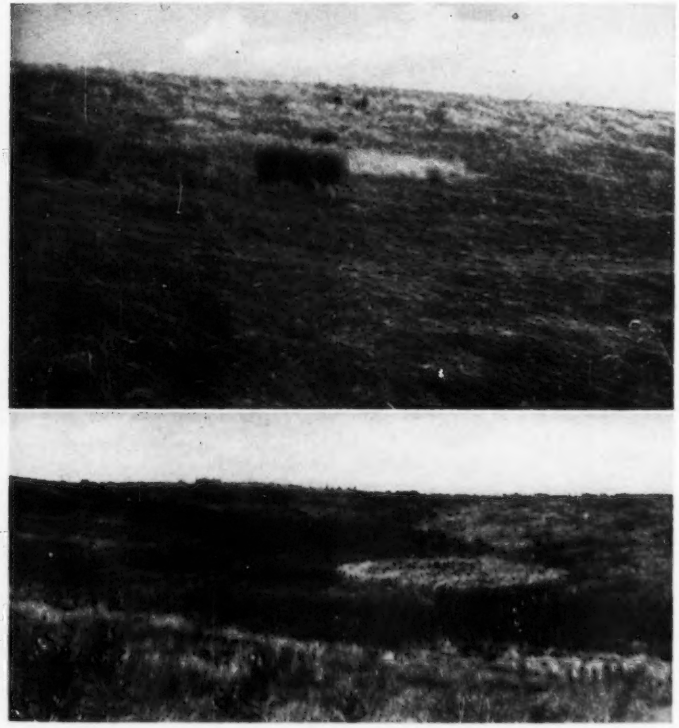

Plate 3.—Highest ridge on tract. Note clone of white sage which has increased appreciably in size. The stand of *Andropogon furcatus* to the left in the lower picture is not included in the earlier view. The general increase in vegetation is apparent from these pictures, and especially the invasion of the blue grass by *Asclepias syriaca*. Top—August, 1937. Bottom—August 16, 1945.

increase in species, with weedy types predominating. Since then there has been an increase in native perennials, a decrease in weeds, though sometimes other weed species have appeared. Plates 3, 4 and 5.

3. Blue grass remains the densest of all species, accounting for one-half to three-fourths of the plant cover on all but a few quadrats.

Frequency

Frequency is the proportional occurrence of a given species in a number of samples. It may be expressed as a percentage, or the results may be distributed in frequency classes. If a given species is found in nine out of ten quadrats its frequency is 90% or it is in frequency class V, (80-100%). It may readily

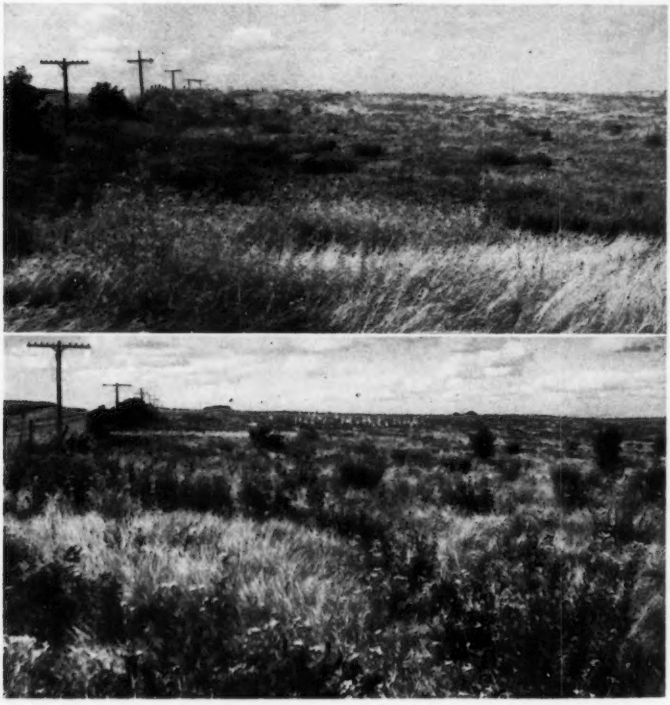

PLATE 4.—General view of Iowa Lakeside Laboratory prairie near west fence. Shows general increase in tall compositae. The apiary in the lower picture was in the tract during 1943 and 1944. Top—August 1937. Bottom—August 17, 1944.

PLATE 5.—Andropogon societies. These pictures indicate that well established prairie showed little change in a four-year interval. They are essentially the same at present. Top—middle section of Iowa Lakeside Laboratory prairie, July 1936. Bottom—north end, August, 1940.

be seen that frequency is an expression of homogeneity of the society; if every sample contained all species; frequency would be 100% for each of them and the stand would be homogeneous.

Frequency gives considerable information concerning the nature of a flora, as some species with very low cover value have high frequency. For example, Liatris and Petalostemum species are colorful plants with extremely slender stems and leaves, hence little cover value, yet no one can deny that the appearance of the prairie at certain seasons is dependent on their relative frequency.

TABLE OF FREQUENCY

	Laboratory tract			
	1938	1945	Knobs 1938	South Prairie 1940
Acer Negundo	13.3	12.5		
Acerates viridiflora var. *lanceolata*				10
Agropyron Smithii	40	37.5		
A. subsecundum	26.6	18.7	10	10
Agrostis alba	6.6			10
Allium stellatum	6.6		20	10
Ambrosia artemisiafolia	80	43.7	100	
A. trifida	6.6	6.2		
Amorpha canescens	6.6	6.2		100
Andropogon furcatus	40	37.5	100	100
A. scoparius	20	18.7	100	100
Anemone cylindrica			10	80
A. patens var. *Wolfgangiana*				30
Asclepias syriaca	6.6	75		
Asclepias verticillata		6.3		
Aster laevis	6.6		10	80
A. ericoides	26.6	37.5	80	
A. ptarmicoides			10	
A. puniceus var. *lucidulus*		6.2		
A. sericeus				10
Astragalus caryocarpus			10	
A. canadensis				20
Bouteloua curtipendula	26.6	6.25	90	70
B. hirsuta			10	
Brauneria angustifolia			20	50
Ceanothus americanus L.				10
Cirsium altissimum (L.) Spreng.				20
C. canescens	46.6	18.7	50	
Comandra Richardsiana Fernald				80
Convolvulus sepium		12.5		
Coreopsis palmata Nutt.				100
Equisetum laevigatum	6.6	6.2		30
Erigeron canadensis	13.3		10	
E. ramosus	13.3		40	
Eryngium yuccaefolium Michx.				50
Gentiana puberula				10
Helianthus grosseserratus		6.2		
Helianthus rigidus				100
Koeleria cristata			10	
Kuhnia eupatorioides	13.3	12.5		30
Lactuca canadensis		6.25		10
Liatris scariosa				80
L. punctata			10	
Linum sulcatum	6.6		10	40
Lithospermum canescens				80
Melilotus alba	13.3	12.5		30
Muhlenbergia cuspidata			70	
Oenothera biennis			10	

TABLE OF FREQUENCY—Continued

	Laboratory tract			South Prairie 1940
	1938	1945	Knobs 1938	
Onosmodium occidentale			10	
Panicum huachucae Ashe				10
P. Scribnerianum				90
Petalostemum candidum				90
P. purpureum		6.25	40	90
Phleum pratense	26.6	12.5	10	
Phlox pilosa				20
Physalis heterophylla	6.6		10	
P. virginiana		6.2		
Poa pratensis	100	100	100	80
Rosa suffulta			20	40
Silphium laciniatum L.				10
Solidago canadensis		12.5		
S. missouriensis				100
S. nemoralis			30	10
S. rigida	6.6	6.25	40	100
S. speciosa var. *angustata*				10
Spartina pectinata	6.6	6.2		
Sporobolus heterolepis			10	
Stipa spartea			10	100
Taraxacum sp.	20	6.2	10	
Tragopogon pratensis		25	20	
Verbena stricta	46.6	12.5	40	
Vicia americana		6.3		
Viola pedatifida	26.6	18.7	30	40

This comparison of frequency shows several interesting facts. First, it bears out the evidence of the permanent quadrats that the flora is extremely stable, showing little change in the past seven years. The only significant developments are in the reduction of common ragweed and proportional increase in Aster ericoides and common milkweed. Second, as compared with the selected knobs, the tract in general has only about 40% incidence of big blue stem and 20% incidence of little blue stem. Every sample taken on the knobs and on the prairie tract to the south contains these grasses. The South prairie is evidently a Stipa prairie as this grass has a frequency of 100%, and though it seems common enough on the laboratory tract, it reaches a frequency of only 10% on the dry knobs, and its occurence is negligible on the tract as a whole.

Other species with high degree of frequency on the prairie to the south are *Coreopsis palmata, Petalostemum* sp., *Panicum Scribnerianum, Lithospermum canescens, Helianthus rigidus* and several others. While these are all present on the laboratory tract, their absence from this frequency table shows the sporadic nature of their occurrence. Several species, mostly of high fidelity,

are found in the south prairie and not in the laboratory tract. This list includes seven such species, and there are others, such as a fine colony of *Habenaria leucophaea* which seems to be on the increase.

Fidelity

A characteristic of certain plants which needs emphasis in connection with the prairie is that of *fidelity*, an expression of the completeness with which a given species is identified with the plant society. An example or two will suffice. *Astragalus caryocarpus* and *Viola pedatifida* are fairly common on upland prairies. So are *Hedeoma hispida* and *Pedicularis canadensis*. The presence of the first two is a far better measure of a prairie than the latter, since *Hedeoma hispida* grows readily as a weed in dry soil, and *Pedicularis canadensis* is a common woodland species farther east. Somewhat rare species of high fidelity are the first to disappear when prairie is disturbed and may be the most difficult to re-establish. Upon their behavior is based the folk belief that prairie, once broken, never reasserts itself. These exclusive plants may well be regarded as the indicators of highly developed prairie; an assemblage of the typical prairie grasses might be considered prairie, but a truly fine prairie includes these exclusive species. The following tables show the species which were included in the list of 1936, those which have appeared since, and those which were seen in the years 1944 and 1945. Species found in the summer of 1935 were not included in the first list. Shimek (6) published a rather complete flora of the region, but did not record any list which may be definitely identified with either of the tracts discussed here.

The following lists of species deal with the status of plants reported in 1936 and with those which have been recorded as appearing in the tract since that time. On the previous list (frequency) seven species not found in the Iowa Lakeside Laboratory prairie are designated by having their author's names cited. These, without exception, are plants of high fidelity to the prairie.

Present status of species growing in Iowa Lakeside Laboratory tract which were reported in 1936

Species	1944	1945	Species	1944	1945
Achillea Millefolium L.		×	*Artemisia caudata* Michx.		
Agropyron repens (L.) Beauv.		×	*A. gnaphalodes* Nutt.	×	×
Agrostis alba L.		×	*Asclepias syriaca* L.	×	×
Allium stellatum Ker	×		*A. verticillata* L.	×	×
Ambrosia artemisiaefolia L.	×	×	*Astragalus canadensis* L.	×	×
A. trifida L.	×	×	*A. caryocarpus* Ker	×	×
Amorpha canescens Nutt.	×	×	*A. hypoglottis* L.	×	×
Andropogon furcatus Muhl.	×	×	*Aster ericoides* L.	×	×
A. scoparius Michx.	×	×	*A. ptarmicoides* (Nees.) T. and G.	×	×
Anemone cylindrica Gray	×	×	*Aster puniceus* var. *lucidulus* Gray	×	×
A. patens var. *Wolfgangiana* (Bess.) Koch					

Present status of species growing in Iowa Lakeside Laboratory tract which were reported in 1936—Continued

Species	1944	1945
Avena sativa L.		
Bouteloua curtipendula (Michx.) Torr.	×	
B. gracilis (HBK) Lag.		
B. hirsuta Lag.		
Brauneria angustifolia (DC.) Heller	×	×
Carex brevior (Dewey) Mack.		
Cirsium canescens Nutt.	×	×
Elymus canadensis var. *robustus* (Scribn. & Smith) Mack. & Bush		
Equisetum laevigatum A. Br.	×	×
Erigeron ramosus (Walt.) B.S.P.		
Euphorbia glyptosperma Engelm.		
Galium boreale L.		×
Hedeoma hispida Pursh		
Helianthus grosseserratus Martens.	×	
H. rigidus (Cass.) Desf.	×	
Heuchera Richardsonii R. Br.	×	×
Hordeum jubatum L.		
Koeleria cristata (L.) Pers.		
Lactuca canadensis L.	×	
Liatris scariosa (L.) Willd.	×	×
L. punctata Hook.	×	×
Linum sulcatum Riddell		×
Lithospermum incisum Lehm.		×
Melilotus alba Desr.	×	×
M. officinalis (L.) Lam.		
Muhlenbergia cuspidata (Torr.) Rydb.	×	×
Oenothera biennis L.	×	×
Oe. serrulata Nutt.		
Onosmodium occidentale Mackenzie	×	×
Oxalis sp. (forms of *O. europaea*)		
Oxybaphus hirsutus (Pursh) Sweet.	×	×
Panicum oligosanthes Schult.		×
P. Scribnerianum Nash		
P. Wilcoxianum Vasey		
Petalostemum candidum (Willd.) Michx.		
P. purpureum (Vent.) Rydb.	×	×
Phleum pratense L.	×	×
Physalis heterophylla Nees	×	×
P. virginiana Mill.	×	×
Poa pratensis L.	×	×
Potentilla arguta Pursh		×
Polygonum convolvulus L.	×	
Portulaca oleracea L.		
Psoralea esculenta Pursh	×	×
Pycnanthemum virginianum (L.) Durand & Jackson		
Ratibida pinnata (Vent.) Barnh.	×	×
Rhus radicans var. *Rydbergii* (Small) Rehd.	×	×
Rosa suffulta Greene	×	×
Scrophularia lanceolata Pursh		×
Setaria viridis (L.) Beauv.		
Solidago canadensis L.	×	
S. gigantea var. *leiophylla* Fern.	×	
S. nemoralis Ait.	×	×
S. rigida L.	×	×
Spartina pectinata Link	×	×
Sporobolus asper (Michx.) Kunth		
Stipa spartea Trin.	×	
Symphoricarpus occidentalis Hooker	×	×
Taraxacum laevigatum (Willd.) D. C.	×	×
T. palustre var. *vulgare* (Lam.) Fern.	×	×
Tragopogon pratensis L.	×	×
Trifolium pratense L.		
T. repens L.	×	×
Verbena stricta Vent.	×	×
Viola pedatifida Don.	×	×

Additions to 1936 List

Species	First seen	1944	1945
Acer Negundo L.	1938	×	×
Acerates viridiflora (Raf.) Eaton	1939		
Agrimonia sp.	1938		
Agropyron Smithii Rydb.	1935	×	×
A. subsecundum (Link) Hitchc.	1937	×	×
Anemone cylindrica Gray	1938		
Apocynum hypericifolium Ait.	1938		×
Asclepias incarnata L.			×
Aster laevis L.	1937	×	×
A. novae-angliae L.	1937		
A. oblongifolius Nutt.	1937	×	×
A. sericeus Vent.	1934	×	×
Chenopodium album L.	1937		
Cirsium arvense (L.) Scop.	1934	×	×
C. discolor (Muhl.) Spreng.	1939		
C. vulgare (Sav.) Airy-Shaw		×	×
Convolvulus sepium L.		×	×
Cuscuta glomerata Choisy	1941		
Erigeron canadensis L.	1938		
Festuca octoflora Walt.	1938		
Fragaria virginiana Duchesne	1937	×	×
Gentiana puberula Michx.	1944	×	×
Helianthus Maximiliani Schrad.	1936	×	×
Kuhnia eupatorioides L.	1937	×	×
Lactuca pulchella (Pursh) DC.			×
L. Scariola L.	1935		
Lithospermum canescens (Michx.) Lehm.			×
Monarda fistulosa var. *mollis* (L.) Benth.	1937	×	×
Muhlenbergia racemosa (Michx.) BSP	1942		
Nepeta cataria L.			×
Panicum virgatum L.	1937	×	×
Phlox pilosa L.		×	
Prunus americana Marsh.	1938		×
Psoralea argophylla Pursh		×	×
Quercus macrocarpa Mich.	1935		
Setaria lutescens (Weigel)) F. T. Hubbard	1937	×	
Solidago glaberrima Martens	1934	×	×
Sorghastrum nutans (L.) Nash	1937	×	
Sporobolus heterolepis Gray		×	×
Verbena hastata L.		×	×
Vicia americana Muhl.	1942	×	
Xanthium commune Britt.	1937		

The fact that all species in the lists were not found in 1944 and 1945 is partly due to the fact that visits were brief in those years, only a week each summer in August. Vernal or autumnal species are likely to be missed in such circumstances. Seasonal differences account for appearance or non-appearance of some plants; 1945 has had a notably cool summer with prairie development nearly a month later than normal in the Lake Okoboji region. The writer can say with confidence that only three prairie species have disappeared from the

tract, namely, *Bouteloua hirsuta, B. gracilis* and *Artemisia caudata.* The latter was close to a cottage area and did not survive human disturbance. The grama grasses belong properly to the short grass plains, or steppes, farther to the west, and were formerly present in small numbers on the ridges of the Laboratory tract. In 1936 they were much damaged by drought, in 1937 were replaced by annuals, such as Festuca octoflora, and have never been seen since. They are still fairly plentiful in some other prairies of the Lake region.

The behavior of plants on this bit of grassland is essentially similar to the findings of Weaver and Albertson (7) in their comprehensive discussion of recovery of grasslands from drought. The exception is the behavior of the grama grasses, and their disappearance is probably due to the fact that they do not compete successfully with the taller grasses.

In August, 1942, two sample plots were burned. These were in the blue grass near the edge of blue-stem prairie societies. It was hoped that this denudation would permit invasion of seeds during the succeeding autumn. When the tract was next examined in August 1944 there was no trace of either of these plots. Effect of the burning was negligible. In the Spring of 1944 an accidental fire swept over the northern part of the tract. It was brought under control by fire companies from neighboring towns. In August the extent of this fire could be traced by charred grass stumps but otherwise not at all. Growth was vigorous with excellent development of all species. Weaver and Fitzpatrick (9) state that occasional spring fires are distinctly beneficial to unmowed prairies, which seems to be verified in this instance.

Invasion of Trees into Prairie

In the past eight years there has been an invasion of trees on the prairie tract. These are mostly box elders, the seeds of which came from the shelter belt to the south. The invasion seems to have followed the dry year of 1936, when plant cover on the prairie was notably reduced. The box elders appeared in 1937, a year which was marked by increase in weed flora. These trees now constitute a vigorous young grove mostly within 200 meters of the shelter belt, but with scattered trees all the way to the fence, $\frac{3}{8}$ mile to the north. Very little prairie flora is affected; most of these trees came into the blue grass community direct. Only in one or two places is a prairie population surrounded by these trees. Eventually these may become typical prairie openings surrounded by timber.

Other invasions by tree species come from the moist parts of the tract. The clonal extension of sand bar willow is conspicuous on the lakeshore, around the springy places and even near the highest part of the tract where a fairly constant water supply is provided by a small kettle hole. Cottonwood and green ash are appearing in these moist-ground thickets. Plates 1, 2, and 6.

Summary

The prairie tract at the Iowa Lakeside Laboratory had reached very nearly its present state of development in 1935. It went through a reduction of cover and of species in 1936 but in 1937 and 1938 was renewed by favorable moist-

ure conditions. During these years 19 species were recognized as new to the tract, and the total species list has changed very little since. A total of forty-two species is added to the published list of 1936; of these twenty-five were seen in 1945.

There has been an increase by clonal expansion of most perennial species, though study of permanent quadrats shows this is very slow. The greatest fluctuation is in the weedy species.

A comparison with a neighboring prairie shows that the stand of vegetation on the Iowa Lakeside Laboratory tract is much less uniform than that of the other prairies. Whether this condition could be changed by controlled pasturing, mowing or fires will require actual experimentation. Species of high fidelity on the Laboratory tract seem to be on the increase, but are still far less abundant than on other neighboring prairies.

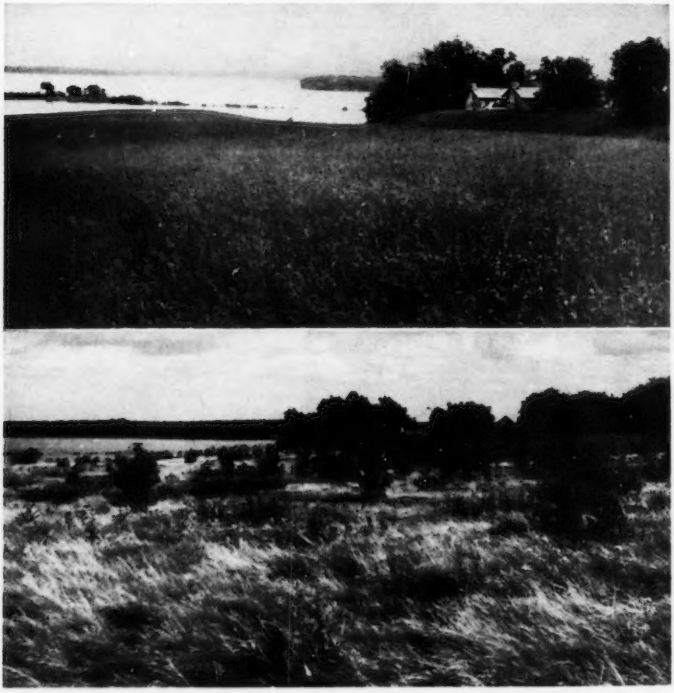

PLATE 6.—Invasion of trees on south end of tract. The boxelder and cottonwood shelter belt is apparent at the right. Upper picture shows nearly pure stand of blue grass which occupied this part of tract. Lower, boxelder invasion. Top—June 1938. Bottom—August 20, 1944.

In parts of the tract a tree succession began in 1937. These trees are developing rapidly and, unless checked by some change of condition, may turn part of the area into woodland.

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Observations on the Desert Gypsum Flora of Southwestern Texas and Adjacent New Mexico

U. T. Waterfall

In his paper on gypsophilous plants of northern Mexico I. M. Johnston (1941) suggests the desirability of studying the plants of similar habitats in southwestern Texas and adjacent New Mexico. The following are preliminary notes concerning the gypsophiles of the latter area. They are based on collections and observations made by the author during August 1942, June and July, 1943, October 1944 and September 1945, principally in Hudspeth, Culberson and Reeves Counties, Texas, and Chaves and Eddy Counties, New Mexico as a part of a more extensive investigation[1] of the desert flora of this region.

The trans-Pecos area of Texas has several large gypsum deposits. One enters Hudspeth County just west of the Guadalupe Mountains, and extends southward about forty-five miles through the Deleware Valley, past Daugherty in Culberson County, to the Baylor Mountains. Around Salt Lake or Salt Flats, southwest of the Guadalupe Mountains, the gypsum forms a fine granulated "sand." East of the Guadalupe Mountains another deposit runs southward, forming a large part of the Culberson Plateau. There are hills near Finley in Hudspeth County from which gypsum is quarried, and numerous beds and ridges in Reeves County. Most of the areas mentioned are shown (as Reeves chalk) on the soil map constituting a part of the *Soil Survey of the Trans-Pecos Area, Texas* (1928).

Collections were taken from various stations in these areas, and also from several other localities including the gypsum flats west of the Pyote Air Base in Ward County, and from gypsum mixed with shale and gravel near the Rio Grande River in Hudspeth, Culberson, Jeff Davis and northwestern Presidio Counties, Texas. In New Mexico the localities studied included gypsum exposures on the Comanchean Bluffs east of the Pecos River near Roswell, and those near Frasier northeast of Roswell in Chaves County, and the gypsum hills and plains south of White's City, Eddy County.

Some of the more common, fairly wide-ranging gypsophiles are: *Sporobolus Nealleyi, Bouteloua breviseta, Selinocarpus lanceolatus, Anulocaulis gypsogenus, Nerisyrenia linearifolia, Mentzelia humilis, Gaura coccinea,* var. *parvifolia, Oenothera Hartwegii* var. *filifolia, Nama carnosum, Coldenia hispidissima, Dicranocarpus parviflorus* and *Sartwellia Flaveriae.*

Examples of other species as definitely gypsophilous, but forming a less prominent element of the vegetation, or having a more restricted range are:

1 Funds to aid in carrying out this project were made available by the Carnegie Institution of Washington and the Arnold Arboretum in the furtherance of their survey of the flora of the desert regions of northern Mexico and adjacent Texas.

Aristida pansa, Tidestromia gemmata, Abronia Nealleyi, Frankenia Jamesii and *Gaillardia multiceps.*

In addition to the species whose distribution seems to be definitely limited to gypsum habitats, there are others that grow as well on gypsum as on other soils. They include *Pappophorum Wrightii* (which may prefer gypsum), *Setaria macrostachya, Mirabilis multiflora* and *Thelesperma megapotamicum.* Many other species infiltrate from surrounding habitats, but do not find gypsum suitable for optimum development. Representative of these species are: *Triodia pulchella, Erigonum rotundifolium, Talinum aurantiacum, Koeberlinia spinosa, Krameria Grayii, Bahia absinthifolia* var. *dealbata* and *Dyssodia acerosa.*

Coldenia hispidissima is perhaps the most abundant species of the desert gypsum, being as characteristic of such areas as *Larrea divaricata* is of the calcareous desert soils of the same region. In this connection it is interesting to note the contrasting behaviour of *Coldenia hispidissima* and *Coldenia canescens.* In the southern end of the Culberson Plateau there are numerous outcroppings of limestone from gypsum beds, *Coldenia canescens* grows on the limestone, while a few inches away *Coldenia hispidissima* will be found rooted in gypsum. I found a northeastward extension of characteristic desert gypsum plants northeast of Roswell, near Frasier in Chaves County, New Mexico, by noticing *Coldenia hispidissima* growing in abundance along the road. Indeed, the species may be considered a definite indicator of the presence of gypsum in soils not immediately recognized as gypseous. I have found small, widely-scattered individuals in gravelly calcareous soils which a careful examination showed to contain small crystals of gypsum. *Mentzelia humilis* behaves somewhat similarly, growing best on gypsum, but sometimes being found on calcareous soils containing varying quantities of gypsum.

The following lists are selected for the purpose of showing the florula of characteristic gypsum stations. From these lists the gypsophiles will be selected and enumerated later in this paper.

Growing on the gypsum beds of the undrained Deleware Valley near Daugherty were the following.

Ephedra Torreyana
Sporobolus cryptandrus
Sporobolus Wrightii
Hilaria mutica
Bouteloua breviseta
Yucca elata
Atriplex canescens
Suaeda suffrutescens
Selinocarpus lanceolatus
Lepidium montanum, var. *angustifolium*
Nerisyrenia linearifolia
Sphaeralcea subhastata
Mentzelia humilis
Cevallia sinuata
Gaura coccinea, var. *parvifolia*
Oenothera Hartwegii, var. *filifolia*
Nama carnosum
Coldenia hispidissima
Lycium Berlandieri
Haplopappus spinulosus, var. *scabrellus*
Haplopappus plurifolius
Thelesperma megapotamicum
Pseudoclappia arenaria
Psilostrophe tagetinae
Gaillardia multiceps
Sartwellia Flaveriae

In the gypsum sand surrounding the Salt Lake southwest of the Guadalupe Mountains were found:

Sporobolus Wrightii
Yucca elata
Atriplex canescens
Allenrolfea occidentalis
Suaeda suffrutescens
Lepidium montanum, var. *angustifolium*
Nerisyrenia linearifolia
Frankenia Jamesii
Coldenia hispidissima
Aplopappus plurifolius
Haplopappus spinolosus, var. *scabrellus*
Aster parvulus
Gaillardia multiceps
Sartwellia Flaveriae

In mid-July, 1943, the gypsum beds in the south end of the Culberson Plateau, thirty to forty miles northeast of Van Horn, yielded the following:

Juniperus monosperma
Bouteloua breviseta
Yucca elata
Anulocaulis gypsogenus
Lepidium montanum, var. *angustifolium*
Koeberlinia spinosa
Rhus microphylla
Sphaeralcea subhastata
Gaura coccinea, var. *parvifolia*
Oenothera Hartwegii, var. *filifolia*
Centaureum calycosum
Gilia rigidula, var. *acerosa*
Nama carnosum
Coldenia hispidissima
Lycium Berlandieri
Haplopappus spinulosus, var. *scabrellus*
Sartwellia Flaveriae
Psilostrophe tagetinae
Dyssodia acerosa
Thelesperma megapotamicum

Juniperus monosperma, *Koeberlinia spinosa* and *Rhus microphylla* are usually found on calcareous soils. Perhaps their abundance at the above station may be accounted for by the presence of limestone strata near the surface. The *Juniperus* is a characteristic feature of the landscape of this area. Dr. I. M. Johnston writes that it is typical *Juniperus monosperma*.

From the gypsum hills near Finley, Hudspeth County, the following were taken:

Aristida pansa
Selinocarpus lanceolatus
Anulocaulis leiosolenus, var. *typicus*
Nerisyrenia linearifolia
Fallugia paradoxa
Mentzelia humilis
Cevallia sinuata
Oenothera Hartwegii, var. *filifolia*
Nama carnosum
Porophyllum scoparium

As noted on the gypsum soils of the Jornada Plain (R. S. Campbell and I. F. Campbell, 1938) the paucity of species on gypsum is sometimes remarkable.

Gypsum beds and exposed gypsum strata alternating with limestone strata in the Panther Hill-Fox Hill area of the central Malone Mountains yielded these species:

Pappophorum Wrightii
Sporobolus Nealleyi
Bouteloua breviseta
Tidestromia gemmata
Selinocarpus lanceolatus
Allionia incarnata
Nerisyrenia linearifolia
Mentzelia humilis
Cevallia sinuata
Gaura coccinea, var. *parvifolia*
Oenothera Hartwegii, var. *filifolia*
Nama carnosum
Dicranocarpus parvifolius
Sartwellia Flaveriae

The alternating strata of limestone and gypsum at this station offered an excellent illustration of the restricted requirements of gypsophytes. Of the species just listed only *Pappophorum Wrightii, Allionia incarnata* and *Cevallia sinuata* grew off the gypsum. *Pappophorum Wrightii* seems more thrifty on gypsum than off it, and *Cevallia sinuata* grows quite well on gypsum.

Contrastingly, on the limestone were found such characteristic species as *Triodia pulchella, Agave lecheguilla, Eriogonum rotundifolium, Acleisanthes longiflora, Allionia incarnata, Acacia vernicosa, Krameria Grayii, Larrea divaricata, Rhus microphylla, Fouquieria splendens* and *Parthenium incanum.*

From Gypsum Flat at the southeastern base of the Malone mountains, about 15 miles west of Sierra Blanca these species were taken:

Aristida Reverchonii
Pappophorum Wrightii
Bouteloua breviseta
Eriogonum rotundifolium
Amaranthus Warnockii
Selinocarpus lanceolatus
Allionia incarnata
Nerisyrenia linearifolia
Mentzelia humilis
Cevallia sinuata
Oenothera Hartwegii, var. *filifolia*
Nama carnosum
Dicranocarpus parviflorus
Haplopappus plurifolius
Bahia absinthifolia, var. *dealbata*
Sartwellia Flaveriae

The locations of the last three stations are well shown on a map by Claude C. Albritton, Jr. (1938).

Extending northward into southeastern New Mexico the gypsophiles already noted are still found to be characteristic of desert gypsum habitats. On gypsum plains and hills four miles south of White's City to the state line, in southern Eddy County were found:

Juniperus Pinchoti
Ephedra Torreyana
Pappophorum Wrightii
Muhlenbergia Porteri
Sporobolus contractus
Sporobolus cryptandrus
Sporobolus Nealleyi
Sporobolus Wrightii
Bouteloua barbata
Bouteloua breviseta
Bouteloua eriopoda
Setaria macrotachya
Mirabilis multiflora
Anulocaulis gypsogenus
Abronia Nealleyi
Talinum aurantiacum
Kallstroemia brachystylis
Polygala alba
Euphorbia Fendleri, var. *chaetocalyx*
Euphorbia strictospora
Euphorbia serrula
Rhus microphylla
Mentzelia humilis
Oenothera Hartwegii, var. *filifolia*
Gilia rigidula, var. *acerosa*
Nama carnosum
Coldenia hispidissima
Viguiera dentata
Psilostrophe tagetinae
Senecio spartioides, var. *Cyparissus*

From gypsum on the Comanchean Bluffs on the east side of the Pecos River, seven miles east of Roswell, Chaves County:

Ephedra Torreyana
Triodia pilosa
Pappophorum Wrightii
Scleropogon brevifolius
Muhlenbergia arenacea
Sporobolus cryptandrus
Sporobolus Nealleyi
Bouteloua breviseta
Tidestromia lanuginosa
Selinocarpus lanceolatus
Anulocaulis gypsogenus
Mentzelia humilis
Gaura coccinea. var. *parvifolia*
Oenothera Hartwegii. var. *filifolia*
Gilia pumila
Coldenia hispidissima
Cryptantha Jamesii
Lycium Berlandieri
Dicranocarpus parviflorus
Thelesperma megapotamicum
Sartwellia Flaveriae
Artemisia Bigelovii
Gaillardia multiceps

This station is about as far east in New Mexico as characteristic desert gypsum flora is known to range. The northeasternmost station known to the author was found on August 27, 1945 near Frasier. Gypsophiles taken here include: *Sporobolus Nealleyi, Bouteloua breviseta, Selinocarpus lanceolatus, Anulocaulis gypsogenus, Nerisyrenia linearifolia, Mentzelia laciniata, Gaura coccinea* var. *parvifolia, Oenothera Hartwegii* var. *filifolia, Coldenia hispidissima, Gaillardia multiceps* and *Sartwellia Flaveriae*. An additional species that showed evidence of being a gypsophile at this station is *Rhus trilobata* var. *pilosissima*.

Farther south I have seen desert gypsophiles as far east as the Pyote Air Base in Ward County, Texas. Here they include: *Bouteloua breviseta, Nerisyrenia linearifolia, Gaura coccinea* var. *parvifolia, Oenothera Hartwegii* var. *filifolia, Mentzelia humilis, Coldenia hispidissima, Gaillardia multiceps* and *Sartwellia Flaveriae*.

Summary of Species Collected on Gypsum

This list summarizes the species taken from numerous stations including those mentioned above. Although it includes plants that are not gypsophiles, it also excludes those unable to live on gypsum. For this reason one does not find such characteristic desert species as: *Yucca macrocarpa, Agave lecheguilla, Acleisanthes longiflora, Larrea divaricata, Fouquieria splendens* and *Parthenium incanum*.

Juniperus monosperma
Juniperus Pinchoti
Ephedra Torreyana
Distichlis stricta
Triodia pulchella
Triodia pilosa
Pappophorum Wrightii
Scleropogon brevifolius
Muhlenbergia arenacea
Muhlenbergia Porteri
Sporobolus contractus
Sporobolus cryptandrus
Sporobolus Nealleyi
Sporobolus Wrightii
Aristida pansa
Aristida Reverchonii
Hilaria mutica
Bouteloua barbata
Bouteloua breviseta
Bouteloua eriopoda
Setaria macrostachya
Andropogon barbinodis
Yucca elata
Eriogonum rotundifolium
Atriplex canescens
Bassia hyssopifolia
Suaeda suffrutescens
Amaranthus Warnockii
Tidestromia gemmata
Tidestromia lanuginosa
Selinocarpus lanceolatus
Mirabilis multiflora

Allionia incarnata
Anulocaulis gypsogenus
Anulocaulis leiosolenus
Anulocaulis reflexus
Abronia Nealleyi
Sesuvium verrucosum
Talinum aurantiacum
Paronychia Jamesii
Koeberlinia spinosa
Lepidium montanum, var. *angustifolium*
Nerisyrenia camporum, var. *angustifolium*
Nerisyrenia linearifolia
Fallugia paradoxa
Acacia vernicosa
Krameria Grayii
Kallstroemia brachystylis
Rhus microphylla
Rhus trilobata, var. *pilosissima*
Polygala alba
Euphorbia Fendleri, var. *chaetocalyx*
Euphorbia serrula
Euphorbia strictospora
Sphaeralcea subhastata
Frankenia Jamesii
Tamarix gallica
Mentzelia humilis
Mentzelia laciniata
Cevallia sinuata
Gaura coccinea, var. *parvifolia*
Oenothera Hartwegii, var. *filifolia*
Limonium limbatum
Centaureum calycosum
Cressa truxillensis
Gilia rigidula, var. *acerosa*
Nama carnosum
Phacelia integrifolia
Heliotropium curassavicum
Coldenia hispidissima
Cryptantha Jamesii
Lycium Berlandieri
Dicranocarpus parviflorus
Haplopappus spinulosus, var. *scabrellus*
Haplopappus plurifolius
Aphanostephus humilis
Aster parvulus
Viguiera dentata
Thelesperma megapotamicum
Pseudoclappia arenaria
Psilostrophe tagetinae
Bahia absinthifolia, var. *dealbata*
Flaveria trinervata
Gaillardia multiceps
Sartwellia Flaveriae
Dysoddia acerosa
Porophyllum scoparium
Psathyrotes scaposa
Artemisia Bigelovii
Senecio Riddellii
Senecio spartioides, var. *Cyparissus*

This list of 90 species presumably corresponds to the list of 62 species found in the White Sands (Emerson, 1935). The larger number in the present enumeration is accounted for by the larger geographic area studied, since it includes the range of such little-known species as *Abronia Nealleyi* and *Anulocaulis reflexus*, and also includes invaders from a larger number of different habitats.

In examining the list one finds several species whose distribution is controlled largely by salinity of the soil. Such plants are: *Distichlis stricta, Sporobolus Wrightii, Atriplex canescens, Suaeda suffrutescens, Sesuvium verrucosum, Tamarix gallica, Limonium limbatum, Cressa truxillensis, Heliotropium curassavicum* and *Pseudoclappia arenaria*. These are usually found in undrained valleys, such as the Deleware Valley, or in areas such as the Pecos Valley where the salt concentration is higher than normal.

In the region studied I have found *Limonium limbatum, and Pseudoclappia arenaria* only on saline-gypseous soils. If these species prefer such a combination of soils throughout their range, they may be properly called halophytic- gypsophiles.

Enumeration of Gypsophiles

PAPPOPHORUM WRIGHTII S. Wats.—I have several sheets of this species from gypsum in Hudspeth and Culberson Counties, Texas, and Eddy and

Chaves Counties, New Mexico. It thrives on such soils, but is also found on calcareous soils.

SPOROBOLUS NEALLEYI VASEY.—Hudspeth Co., Texas. Gypsum Flat southeast of Malone Mts., 5799; gypsum in central Malone Mts., 5823. Chaves Co., New Mexico. Gypsum on Comanchean Bluffs, 7 miles east of Roswell, 5710: gypsum ½ mi. southwest of Frasier, 6177.

The collection numbers referred to above, and in the remainder of this enumeration, are the author's. Duplicates of the majority of specimens are in the Gray Herbarium, and in the herbariums of the New York Botanical Garden and the Missouri Botanical Garden.

Sporobolus Nealleyi has been found by the author only on gypsum. It is a characteristic species of many gypsum localities.

ARISTIDA REVERCHONI Vasey.—Hudspeth County. Gypsum Flat southeast of Malone Mts., 5788. This species was fairly common at this station. Its distribution was limited to gypsum.

BOUTELOUA BREVISETA Vasey.—I have found this *Bouteloua* to be of widespread occurrence on gypsum, where it is a characteristic species, but I have not found it on adjoining soils. The following are selected from among other collections I have.

Hudspeth Co. Gypsum in central Malone Mts., 5819. Culberson Co. East of Daugherty, 5184. Eddy Co., N. Mex. Gypsum hills 3 miles north of state line, 5737. Chaves Co. Gypsum southwest of Frasier, 6135.

TIDESTROMIA GEMMATA Johnston.—Hudspeth Co. Gypsum in the Panther Hill-Fox Hill area of the central Malone Mts., Oct. 11, 1944, No. 5821.

Johnston (1943) described the species from gypsum in Coahuila. A collection from the Big Bend (Boquillas, Brewster Co.) was later referred by him to *T. gemmata* (Johnston, 1944). The present collection represents a considerable northwestward extension of range, and offers additional evidence showing the gypsophily of the plant.

SELINOCARPUS LANCEOLATUS Wooton.—Hudspeth Co. Gypsum hills near Finley, 5028, Gypsum Flats southeast of the Malone Mts., 5790. Culberson Co. Gypsum in the Deleware Valley near Daugherty, 4121, 5028 and 5179. Chaves Co., New Mexico. Gypsum southwest of Frasier, 6138. I have seen the species in southern Eddy Co. on the gypsum south of White's City.

These records extend the known range of this obligate gypsophile considerably southward and northeastward from the White Sands—northwestern Culberson County region from which it has been previously known (Johnston 1941).

ANULOCAULIS GYPSOGENUS Waterfall.—To the distribution already shown by the author (1945) may be added: gypsum southwest of Frasier, Eddy Co., 6131. The species grew abundantly at this station which is as far north as it is now known to occur. It is a definite gypsophite growing nowhere except on gypsum.

ANULOCAULIS LEIOSOLENUS (Torr) Standl. var. TYPICUS Waterfall.—This is the little-known localized plant of gypsum habitats in Hudspeth Co. (Waterfall, 1945).

ANULOCAULIS REFLEXUS Johnston.—Jeff Davis Co. Gypsum about 11 miles southwest of Chispa, 5296. This collection represents this recently described (Johnston, 1944) Mexican gypsophile at the northern limit of its range.

ABRONIA NEALLEYI Standley.—Eddy County, New Mexico: Gypsum plains and hills south of White's City near the Texas State Line, 5723 collected in 1944, and 6194 taken in 1945.

This rare species appears to be a definite gypsophile. From the above locality it presumably extends eastward to Screw Bean, Reeves County, Texas where the type was collected by Nealley (Standley, 1909). It should be found on the great gypsum beds of northern Culberson County.

LEPIDIUM MONTANUM Nutt., var. ANGUSTIFOLIUM C. L. Hitchcock.—I have found this species at a number of gypsum stations indicating that it is at least gypsum-tolerant, if not actually gypsophilous. It seems to occur where the salt concentration is higher than normal as in the Pecos Valley, and in various playas.

NERISYRENIA LINEARIFOLIA (Wats.) Greene.—I have a number of collections of this species from localities extending from the Gypsum Flat southeast of the Malone Mts. in Hudspeth County, eastward through Culberson and Reeves Counties to the gypsum near the Pyote Air Base in Ward County, and northward through Eddy County, New Mexico, to the gypsum near Frasier in Chaves County.

KALLSTROEMIA BRACHYSTYLIS Vail.—Ward County, Texas. Gypsum flats west of Pyote Air Base, 5492. Eddy County, N. Mex. Gypsum 3 miles north of Texas line, 5739.

Although growing well on gypsum this species may be gypsum-tolerant, rather than gypsophilous.

RHUS TRILOBATA Nutt., var. PILOSISSIMA Engl.—This shrub behaved as a gypsophile at the only locality from which I have collected it, near Frasier in Chaves County, New Mexico.

EUPHORBIA FENDLERI T. & G., var. CHAETOCALYX Boiss.—Although apparently not limited to gypsum, this woody-based *Euphorbia* is often common on such sites. I do not find it on the adjoining calcareous deserts.

SPHAERALCEA SUBHASTATA Coulter.— I have a number of sheets from gypsum and gypseous-limestone soils. It also grows on calcareous soils, but prefers the former.

FRANKENIA JAMESII Torr.—Hudspeth Co. Gypsum sands around Salt Lake southwest of the Guadalupe Mts., 3819 and 4485.

This species is abundant at the above locality, but I have not found it elsewhere. It is definitely restricted to the gypsum sands of this site.

MENTZELIA HUMILIS (Gray) Darl.—Hudspeth Co. Gypsum near Finley, 5021. Culberson Co. Gypsum ridges near Daugherty, 4125 and 4469. Ward

Co. Gypsum flats west of Pyote Air Base, 5498. Eddy Co., N. Mex. Gypsum south of White's City near Texas line, 5732.

This species grows in the strongest concentrations of gypsum. It also occurs in calcareous gravelly soils having small quantities of gypsum. It may then serve as a gypsum indicator, as does *Coldenia hispidissima.*

MENTZELIA LACINIATA (Rybd.) Darl.—Chaves Co., N. Mex. Gypsum on Comanchean Bluffs 7 miles east of Roswell, 4286: gypsum near Frasier, 6137.

CEVALLIA SINUATA Lag.—I have found this species occasional, but thrifty on gypsum. Evidently it is gyp-tolerant.

GAURA COCCINEA *Nutt.,* var. PARVIFOLIA (Torr.) T. & G.— I find this plant characteristic of gypsum from Hudspeth County through Culberson and Reeves Counties, Texas, north through Eddy County to the Roswell area of Chaves County, New Mexico.

OENOTHERA HARTWEGII Benth., var. FILIFOLIA (Eastw.) Munz.—Hudspeth Co. Finley gypsum, 5023; central Malone Mts., 5830; gypsum flats southeast of Malone Mts., 5800; Culberson Co. Gypsum near Daugherty, 4122 and 5196. Reeves Co. Gypsum ridge 25 miles north of Pecos, 5490. Ward County. West of Pyote Air Base, 5494. Eddy Co. New Mexico. Gypsum south of White's City, 5729. Chaves Co. Near Frasier, 6136.

The above representative citations are of a linear-leaved gypsophilous *Oenothera* which I belive is referrable to the var. *filifolia.* On calcareous soil the typical variety is found. No. 5023, from the gypsum near Finley, approaches the typical variety.

LIMONIUM LIMBATUM Small.—Reeves Co. Gypsum in the Pecos valley north of Pecos, 4210 and 4373. Chaves Co., New Mex. Saline gypsum flat 13 miles northeast of Roswell, 6178.

The soil at both these localities is salty as well as gypseous. This species is not found on dry, non-saline gypsum beds.

NAMA CARNOSUM (Woot.) Hitchcock.—Hudspeth Co. Gypsum east of Finley, 5022; gypsum southeast of Malone Mts., 5787. Culberson Co. Gypsum near Daugherty, 4474, 5197, 40 miles northeast of Van Horn, 5006. Eddy Co., New Mex. Gypsum hills south of White's City, 5740.

This species is found only on gypsum. It is fairly common in the areas indicated above.

COLDENIA HISPIDISSIMA (Torr.) Gray.—This species is characteristic of xeric gypsum beds in the region studied, often forming a prominent part of the vegetation. I have found a few scattered specimens on gravelly calcareous soils, but in each case a careful examination showed the presence of varying quantities of gypsum crystals.

DICRANOCARPUS PARVIFLORUS Gray.—Hudspeth Co. Gypsum Flat southeast of Malone Mts., 5793: Chaves Co., N. Mex. Gypsum on Comanchean Bluffs east of Roswell, 5706.

HAPLOPAPPUS PLURIFOLIUS (T. & G.) Hall.—This species is characteristic of gypsum, although found on other soils.

HAPLOPAPPUS SPINULOSUS (Pursh.) DC., var. SCABRELLUS (Greene) Blake.—This plant grows well on gypsum, and seems to be more often found there than elsewhere.

THELESPERMA MEGAPOTAMICUM (Spreng.) Kuntze.—In the region studied this species is characteristically found on gypsum, and is more abundant there than on other soils.

PSEUDOCLAPPIA ARENARIA Rybd.—Culberson Co. Gypsum ridge north of Salt Lake near Daugherty, 4120; gypsum along saline playa, 1 mile east of Daugherty, 5194; Reeves Co. Saline gypsum north of Pecos, 4212 and 4379.

This species appears to behave as a halophytic-gypsophile.

PSILOSTROPHE TAGETINAE (Nutt.) Greene.—A phytoentity that may be referrable to this species is found on gypsum, especially in Culberson County.

GAILLARDIA MULTICEPS Greene.—Hudspeth Co. Gypsum sand, Salt Lake, 3824, 4486, 5199; Culberson Co. Granulated gypsum east of Daugherty, 5194: Reeves Co. Gyp ridge 25 miles north of Pecos; Ward Co. Gypsum flat west of Pyote Air Base, 6372; Chaves Co., N. Mex. Comanchean Bluffs east of Roswell, 4288; southwest of Frasier, 6134.

I have found this species restricted to gypsum. The Hudspeth County collections are from near the former site of Ables where it was collected by Cory. However, the collection north of Pecos and the one near the Pyote Air Base represent considerable eastward extension of range, while those in Chaves County, New Mexico are quite a bit north of Standley's collection from near Carlsbad cited by Johnston (1941) as the only collection known from New Mexico.

SARTWELLIA FLAVERIAE Gray.—Hudspeth Co. Gypsum sand southwest of Guadalupe Mts., 3826; central Malone Mts., 5825; southeast of Malone Mts., 5792. Culberson Co. 40 miles northeast of Van Horn, 5005; Reeves Co. 1 mile north of Pecos, 4376; Chaves Co., N. Mex. Gypsum southwest of Frasier, 6150.

I have collected this species only from gypsum, or gypseous soils, supporting Dr. Johnston's suggestion (1941: 168) that it is confined to such soils.

SENECIO SPARTIOIDES T. & G., var. CYPARISSUS Greenman.—Eddy Co., New Mexico. Gypsum 3 miles north of Texas line near U. S. Highway 62, No. 5742.

This species was identified for me by Dr. Greenman. It was first collected by me on Oct. 9, 1944. Collecting again in the same locality on Aug. 28, 1945. I found it fairly common, distinguishable by its characteristic growth habit although it was not then in flower. It was restricted to gypsum at this station.

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Observations on the Biology of the Snail Lymnaea stagnalis appressa During Twenty Generations in Laboratory Culture

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Introduction

During the course of the last one hundred years various notes and papers have appeared presenting observations on the life history and culture of numerous lymnaeids; in the last two decades the emphasis of the research on this subject has been placed increasingly on an experimental investigation of the factors governing growth. A review of the results of these investigations indicates that *Lymnaea* is well adapted to serve as a dependable, easily handled, normal, healthy, experimental mollusc of conveniently small size, of short life cycle, and available in quantity and in various stages of development throughout the year. This genus is endowed with further desirable qualities: many of its species occur over a wide geographic range, are fairly constant in form, have been popular laboratory material for over eighty years (certain species such as *L. stagnalis* have been studied more intensively ecologically, physiologically, histologically, morphologically than any other basommatophoran pulmonate), and are probably the highest form of animal life in the evolutionary series in which self-fertilization occurs (Baily, 1931). In the parasitological field, these snails are also important as vectors of parasites of man, domestic animals, wild game and fish. In this connection, Krull (1931) in a paper on the importance of laboratory-raised snails in helminthology, writes: "Life history studies are rapidly occupying the attention of the helminthologists throughout the world, and this phase will soon be on a par with taxonomic investigations in the group. The snail is almost indispensable in life history work on trematodes."

In an effort to develop further the potentialities of *Lymnaea* as an experimental gastropod, this paper attempts, through the integrated contributions of numerous earlier researchers and by additional original investigation on *L. stagnalis appressa* Say to present a simple, inexpensive, reliable method for culturing it in quantity. Observations on the life history of *L. s. appressa* cultured in this laboratory for twenty generations over a period of six years are also reported. This snail, besides its excellent response to laboratory culture, has the added characteristic advantage of possessing a relatively thin semi-transparent shell which permits inspection of many of the internal organs in the living, undisturbed animal.

Certain environmental conditions have been described in the literature as improving growth and fertility in lymnaeids. Boycott (1936) in studying the native habitats of freshwater Mollusca in Britain, came to the conclusion that "the more important features of favorable habitats are (1) cleanliness of

water, (2) absence of disturbance and (3) presence of lime." The most populous habitats were calcium-rich rivers, lakes and canals. Goetsch (1928) showed that the factors which interfere with growth and development of aquatic animals are twofold: chemical and mechanical. Most important among the chemical factors were the excretions resulting from metabolism and the food residues, either uneaten or ejected after more or less digestion. Among the mechanical factors were interference through the increase of numbers of individuals resulting in restlessness and increased use of energy. Other factors were the nature and digestibility of food, the way the food was given and conditions which affected eating.

There has been little agreement as to the minimum volume of water required to enable a single snail to grow to full size. Colton (1908, 1912) estimated 5 liters; Turner (1927), 10-15 cc.; Colton (1934), 400 cc. (in which he raised ninety-three generations); Forbes and Crampton (1942a), 500 cc.; Crabb (1929), 150-175 cc.; and Baily (1939), 100 cc. (A list of investigators and their research animals is given at the end of this historical review.) Often in this work the debatable inference has been given that less water means smaller snails. In the mass culture of snails it is important to know the minimum volume of water per snail which will produce optimum growth. There is as yet no answer to this question. Turner (1927) thought that the rate of growth of snails brought up in standard jars was a function of their numbers. Forbes and Crampton (1942a) found that the larger the number of snails per culture, the smaller the average size of members of the association.

There is some controversy as to the extent of cutaneous respiration in *Lymnaea*, and correspondingly the practicability of aeration of snail cultures. Crabb (1929) and Colton (1934) both emphasized the almost complete dependence of these snails on atmospheric air for their oxygen supply. However Walter (1906) and Willem (1896) both considered the presence of an adequate oxygen supply in the water conducive to improved growth. The observations of the following investigators lends greater importance to cutaneous respiration and the necessity for aeration of mass snail cultures: Cheatum (1934) in ecological studies found that *Lymnaea* migrated into deep water in the winter and that all snails collected at that time had water in the lungs. Precht (1939) noted that this snail changed to total cutaneous respiration when the temperature of the water dropped below 5° C. Sonehara (1935) imprisoned *Lymnaea* under water for extended periods. Noland and Reichel (1943) carried *Lymnaea* through the complete life cycle at room temperature without access to air; the lungs of the snails were filled with water at all times. Crabb (1929) writes that aeration promotes growth through reducing foulness of the water and by oxidizing decaying substances.

Some question exists as to the depth of container best suited for culture, as some investigators have implied that shallow aquaria with large surface area give optimal results. However, such species of *Lymnaea* as *stagnalis* which occur natively in the more open bodies of water live equally well in either deep or shallow water (Cheatum, 1934; and in Galtsoff, 1937). Krecker (1933) found *Lymnaea* abundant to numerous down to a depth of eighteen inches on the western shores of Lake Erie in the summer.

It has generally been recognized that calcium is essential to the growth of the shelled gastropods. Boycott (1936) stresses the importance of lime in the native environment of aquatic snails. Colton (1908) found that calcium sulfate was particularly beneficial to the growth of *Lymnaea* in the laboratory. Boycott et al. (1932) placed lymnaeids previously growing natively in very soft water in cultures of hard water (about 70 mg. Ca per liter); the original parents of about 5 mm. in length and 1 mg. in weight gave descendants (three years later) about 12 mm. in length and 66 mg. in weight. Krull (in Galtsoff, 1937) states that calcium carbonate (comparable to "Baker's Analyzed") is not only desirable but seems almost indispensable in the rearing of aquatic snails.

Manganese is found in plants and animals and seems to belong to the "essential" group of chemicals. Only one reference has been found to this in the basommatophorans. Hiltner (1926) in floricultural experiments noted that at the end of nine months the number of *L. stagnalis* in an aquarium containing a trace of $MnSO_4$ was four times that in untreated aquaria.

As regards the optimal hydrogen ion concentration for lymnaeid growth, Walton and Wright (1926) found *L. truncatula* occurring natively over a pH range of 6.0 to 8.6, and *L. peregra* 5 8 to 8.8. Atkins and Lebour (1924) recording only sixteen tests of snail inhabited waters over a wide area, found a pH range of 6.4 to 7.8 and 6 6 to 7.7 for these same snails. Krull (in Galtsoff, 1937) says that snails apparently thrive best in alkaline water, and no success has been had in using acid water.

Krull (in Galtsoff, 1937) states that snail aquaria should never be kept in sunlight but in subdued light. Crabb (1929) after preliminary experiments stated that direct sunlight did not appear to increase the growth rate over that of sunlight which had passed through plate glass, but that total absence of light inhibited growth somewhat.

Some discussion has appeared on the effect of fouling on growth in these snails. Legendre (1907, 1908) noted that clean cultures favored the growth of snails and that excrement, especially the liquid kind, retarded growth. Colton (1908) showed that it was not the fecal matter in the aquarium that hindered growth, as accumulated fecal pellets when washed and filtered had a beneficial effect on growth. Also, that weak solutions of waste products of metabolism were beneficial. Goetsch (1928) showed that chemical excretions resulting from catabolism retarded growth and development. Crabb (1928) indicated that foul media inhibited oviposition, and (1929) that food insufficiency and foul media were the most common growth-inhibiting factors in snails reared in otherwise favorable media. Boycott (1936) believes that clean water makes a more favorable habitat. Popovici-Baznosanu (1921) seemed to think that excreta slightly favored growth.

It is generally agreed that sand is an indispensable item in achieving optimal growth in snails because of the need for the proper trituration of food in the gizzard. Sand particles have been observed in the gizzard of lymnaeids by many investigators, but Colton (1908) and Heidermanns (1924), principally the latter, showed its importance. Such investigators as Forbes and Crampton (1942a, 1942b), Colton (1908, 1918; in Galtsoff, 1937), Sonehara (1933),

speak of placing traces of fine sand, mud or garden soil in the aquaria to provide the needed grit.

The kind of food providing optimal growth in these snails has been only slightly investigated. Earlier workers depended upon the native aquatic vegetation (Algae, *Chara, Elodea, Lemna, Cabomba,* etc.) as a source of snail food. Popovici-Baznosanu (1921) thought that of all foods the most important was microflora. Dried leaves have been used by some investigators with some success (Colton, 1908, etc.). Sonehara (1933) found spinach a good food. Loose, green, leaf lettuce, however, has been used most commonly by the majority of the more recent researchers: Popovici-Baznosanu (1921), Turner (1927), Crabb (1929), Baily (1931, 1939), Imai (1937), Winsors (1932, 1935), Forbes and Crampton (1942, 1942b), and others. Crabb (1929) found that in addition to the lettuce, a diet of boiled wheat grains and filter paper produced the best results in growth and in number and viability of eggs laid. Popovici-Baznosanu (1921), Turner (1927), Piersanti (1931) and Baily (1939) agree that the food supply is the important factor in determining the size to which a snail can grow.

The study of the vitamin needs of basommatophorans has been started by Forbes (1942), who found that small amounts of vitamin B_1 added to the standard diet of *L. columella* exerted a stimulating effect on growth and fertility, while larger amounts retarded these functions of the organism; there was some evidence (possibly due to dietary imbalance) that the life cycle was shortened significantly in both instances.

A few papers have appeared in the literature on the effects of temperature on the hatching time and growth of lymnaeids. Imai (1937) in a study of the growth of the larval shell of *L. japonica* under controlled temperature conditions, noted that higher temperatures resulted in the acceleration of development but that final size was diminished at both the first and the second cycle of growth. Vaughn (1944) in a detailed investigation of the effects of temperature upon the hatching time of the eggs and upon the growth of young *L. stagnalis appressa* under controlled conditions, found that a temperature of 20° C. was the optimum constant temperature for growth, and that his growth curve obtained at this temperature compares favorably with the corresponding parts of the sigmoid growth curves for this species determined by Semper (1874, 1881) and Crabb (1929).

The number of workers who have reared basommatophorans in the laboratory is large. Their methods for the most part have involved simply the use or finger bowls or small balanced aquaria. The following table is an attempt to tabulate workers who have reared these snails in the laboratory, the species of snail grown and the number of generations successfully reared, where this was available.

Hogg	(1854)	*L. stagnalis*
Semper	(1874, 1881, 1883)	*L. stagnalis*
DeVarigny	(1894)	*L. stagnalis*
Willem	(1896)	*L. ovata*
Legendre	(1907)	*L. stagnalis*
Legendre	(1908)	*L. auricularis*
Walter	(1906)	*L. elodes*

Holzfuss	(1914)	*L. stagnalis*	(4 generations)
Künkel	(1908)	*L. stagnalis*	
Colton	(1908–1934)	*L. columella*	(93 generations)
Popovici-Baznosanu	(1921, 1928)	*L. stagnalis*	(3 generations)
Agersborg	(1924)	*Physa gyrina*	
Hiltner	(1926)	*L. stagnalis*	
Seshaiya	(1927)	*L. luteola*	
Turner	(1927)	*L. stagnalis*	
Turner	(1927)	*L. peregra*	
Sonehara	(1933, 1935)	*L. japonica*	
Rumiantsev	(1928)	*L. stagnalis*	
Walton and Jones	(1926)	*L. truncatula*	
Crabb	(1927–1931)	*L. stagnalis appressa*	
Krull	(1931)	*Gyraulis parvus*	
Baily	(1931, 1939)	*L. columella*	
Boycott et al.	(1930)	*L. peregra*	
Winsors	(1932, 1935)	*L. columella*	
Imai	(1937)	*L. japonica*	
Forbes and Crampton	(1942a)	*L. palustris*	(3 generations)
Forbes and Crampton	(1942b)	*L. palustris*	(7 generations)
Forbes	(1942)	*L. columella*	
Noland and Reichel	(1943)	*L. stagnalis appressa*	(2 generations without access to air)

Culture Methods

The need for considerable numbers of snails for experimental work in this laboratory necessitated the development of a method for growing snails in large numbers in a relatively small space and under conditions which permit the following of generation after generation in the laboratory. Developing a culture method of this sort has necessitated a more accurate understanding of the various environmental factors influencing the snail in laboratory culture. Some of these factors have been investigated to some extent by previous workers. An attempt is made herein to review and integrate their results with the findings of the present authors.

Some six years of laboratory research on *L. s. appressa* have yielded relatively simple and inexpensive methods of culture. One to three gallon, cylindrical, clear glass battery jars provided suitable aquaria; we have found the one-gallon jars the most convenient to handle. These were placed on built-in shelves in large northern windows in indirect sunlight. Such containers were easily cleaned and the snails within could be conveniently observed. Squares of ordinary window glass were utilized as covers. A small notch carefully chipped with a glass cutter in the middle of one side of the cover supplied an opening for entrance of the aerator tubing. Covers were necessary to avoid excessive evaporation and escape of the snails. Two small electric Marco air pumps, each with an air capacity of approximately one liter per minute, supplied the necessary air for oxygenation of the aquaria water. Rubber tubing conducted air to each aquarium. A two-quart glass bottle installed in the system eliminated the pulsation effect of the pump and equalized the flow of air to the air releasers. Metal "T's" (being less fragile than glass) were employed for connecting subsidiary lines to the main air lines. Short U-tubes of

copper led the air over the top edge of each aquarium and through the notch in the glass cover. Rubber tubing was forced up over the inner segment of the U-tube to prevent contact of the aquaria water with the copper. From the copper U-tube the rubber tubing extended half way down inside the aquarium and had at its end a glass tube which was bent in the shape of a letter U or L with an air releaser on its upturned tip. In the large jars the tube and releaser were held down to the bottom of the aquarium by being embedded in concrete which had been moulded around the glass tubing and allowed to set so as to fit in the angle between the bottom and side of the aquarium jar. Care was exercised to prevent the water in the aquarium from coming in contact with the copper tubing. Copper ions, even in high dilutions, are strongly toxic to *L. s. appressa.*

The air releasers sent a constant stream of very finely divided air bubbles into the aquaria. The releasers eventually adopted were constructed in the laboratory: they consisted of small wooden discs, about 1/4 inch in thickness and 3/4 inch in diameter, and were held in the end of a short piece of rubber tubing of the proper size to fit tightly around the wooden discs. Short pieces of rubber tubing of progressively smaller diameter were fitted into the original section of the larger tubing to adapt the opening in the lower end of the releaser to that of the upturned glass tube at the bottom of the aquarium. The circular wooden discs were sawed from commercial 3/4 inch birch dowelling (the best of several woods tried) which can be secured at lumber yards in several diameters. This type of releaser is very inexpensive and quickly made. Several of the commercial types of metal, cement, porous sandstone, felt cloth, etc., air releasers were tried but were found less satisfactory. The wooden releasers require replacement every two or three months as the surfaces of the wood exposed to the water slowly rots. Scraping of the exposed surface of the releasers about once a week is necessary to keep them in good working condition.

Aeration by plants was also tried. *Vallisnera* was found to be the most satisfactory aquarium plant. The long slender leaves continue to grow throughout the year and provide good "ladders" on which the snails may crawl to the surface for air. The plants, fertilized by the fecal depositions of the snails, tend to crowd the space in the aquarium and must occasionally be thinned out. *Elodea, Ceratophyllum, Myriophyllum* and the narrow-leaved Potamogetons were tried with less success. Continued experimentation has shown that plants are quite unnecessary in the aquaria, provided artificial aeration can be supplied constantly. The latter is far more expedient, particularly in special feeding experiments where foreign food substances are undesirable. The absence of vegetation also facilitates cleaning of the tanks. For this reason the use of aquarium plants has been for the most part discontinued. Thorough oxygenation of aquarium water not only provides sufficient oxygen for the snails, but maintains water currents and keeps putrefaction of fecal material and waste food at a minimum. *L. s. appressa,* although possessing a lung, still depends upon cutaneous respiration to a great extent. Sand or fine gravel were frequently placed in the tanks to provide the particulate matter necessary for the proper trituration of food by the snail gizzard.

Green, loose, leaf lettuce was in general found to be the best food for this pulmonate. Wheat cereal cooked with milk and with a small amount of salts added (those normally found in snail blood) was also excellent, particularly in increasing the size and number of egg masses. Green lettuce alone, plus the algal and protozoan coating on the inner surfaces of the aquaria, however, appears to provide all the necessary nutritional elements required in the normal development of the snail. Up to the present some twenty generations have been grown on the lettuce-wheat diet. Apparently the digestive system of this gastropod does not succeed in drawing all the nutritional value from the food in the first passage through the tract, since the fecal material is reconsumed several times by the snails and becomes progressively darker as it is worked over. The cooked wheat cereal was supplied in feeders floated on the surface of the aquaria along with the washed green lettuce leaves. These feeders were made by attaching a curved strip of aluminum to the under side of a square of cork forming a semi-cylindrical space into which the cereal (cooked thick with half milk and half water) could be pressed.

Water in the aquaria was changed as often as required to keep the snails in good condition for the experiments. In special experimental work the water sometimes required daily changing; the greater the number of snails in the tank the more frequent were the changes. With only ten to fifteen adult snails in ten liters of artificially aerated water, changing was not necessary for more than a month. The snails themselves by eating their own feces and the algal growths on the aquaria walls helped in keeping the tanks clean. It was not necessary to clean out the aquaria completely each time the water required changing: siphoning off the old water and adding fresh was frequently sufficient.

A snail-saving procedure was developed for changing the water in aquaria filled with very young snails. The contents of the aquarium were poured through a cloth of open texture (as cheese cloth, marquisette or organdy) spread upon a holder of window screening about eight inches in diameter. The snails and the grosser particles of debris remained on the cloth; after slight rinsing, the cloth with the snails could be removed from the screen holder and washed off into a clean aquarium by immersing the cloth in the water of the freshly filled jar. When very young snails had to be transferred individually to new containers, a camel's hair brush was found to be the most suitable means of transfer.

Water for the aquaria was taken from the city supply which comes from artesian wells 700 to 840 feet deep, is heavily charged with mineral salts and is slightly chlorinated. Colorimetric tests with the ortho-tolidine reagent (Ellms and Hauser, 1913) showed that the free chlorine present was negligible in amount. Tests on the fresh water in the aquaria shortly after aeration commenced, disclosed that free chlorine is soon driven off. In the twenty generations of *Lymnaea* raised, no noxious effects have been noted from the water used.

Through the courtesy of the Madison (Wisconsin) Board of Health an analysis of the city water, used in the snail research, has been obtained for the year 1944. Much of the success of these snail cultures has undoubtedly been due to the high calcium and magnesium content of the water:

Table 1.—Complete Chemical Analysis of City of Madison Drinking Water (composite of all the city wells)

	p.p.m.
Total Solids	336.0
Calcium as Ca	71.0
Magnesium as Mg	33.56
Sodium and Potassium as Na	4.97
Iron as Fe	0.32
Silica as SiO_2	11.30
Sulphates as SO_4	11.73
Chlorides as Cl	3.70
Nitrates as NO_3	0.001
Alkalinity (Methyl Orange) as $CaCO_3$	298.3
Alkalinity (Phenolphthalein) as $CaCO_3$	0.0
Total Hardness as $CaCO_3$	341.0
Carbonate Hardness as $CaCO_3$	42.7
Free Carbon Dioxide as CO_2	13.5
pH value	7.9
Ammonia Nitrogen	0.03
Organic Nitrogen	0.09
Fluorine	0.0

As indicated in Table 1 the pH of the city water has been about 7.9 The pH of the water, determined on the glass electrode, in healthy aquaria over many weeks remained always on the alkaline side: ranging approximately between 7.2 and 8.6. Variation was found to correspond in part with concentration of waste materials (tending toward acidity) and with the extent of photosynthesis of phytoplankton and plants (producing alkalinity).

The temperature of the water in the tanks varied with that of the air in the windows where they were placed, generally 17.5 to 21° C. Temperatures as low as 15° C. were experienced in cold winter spells and did not appear to harm the snails, although it did materially slow their feeding and growth.

It was found necessary during the winter months to warm the water to room temperature when changing it. Fresh water from the city supply was found to reach temperatures as low as 10° C. Placing snails in this cold water seemed to retard growth sufficiently to produce a noticeable deformation (growth check) on the shell corresponding to each time of changing into fresh, cold aquarium water.

After a culture tank has been standing some time without changing, the water becomes a light greenish-brown, and large numbers of Phytomastigina, Chlorophyceae, diatoms, desmids, *Lacrymaria, Paramecia, Coleps, Chilomonas, Euplotes, Euglena, Vorticella, Stentor,* bacteria, *Protococcus*-like green cells, *Planaria,* minute nematodes, Rotifera, *Daphnia, Clyclops,* ostracods, *Chaetogaster limnaei,* etc., appear. A very heavy growth of these forms does not seem harmful to the snails. Densest growths appear when the days start getting longer in March. *C. limnaei,* ectocommensals on the snails, appeared and disappeared in cycles in the earlier years of the culture, sometimes becoming so abundant that the fleshy parts of the snails appeared hairy, particularly the

fleshy extensions of the propodium around the lips. This annelid has been found on all external parts of the snails and some even have been traced to the respiratory chamber. They appear to have no harmful influence on their hosts. Wagin (1931) also found this annelid in the lung of lymnaeids, each mollusc harboring 70-100 worms, sometimes up to 900, and yet the worms seemed to occasion the host no harm. In the last few years of the culture these worms have not been noticeably present.

Aquaria similar to those used for the adult snails were utilized in hatching eggs and growing the young snails. Egg masses were scraped with a razor blade from the surface of the tanks of the ovipositing snails (care being taken that the ootheca of the egg mass was not ruptured) and placed on the bottom of newly cleaned aquaria. The young snails were left in these nurseries with thorough aeration until they had grown to the point where they could be transferred to new tanks without danger of loss or injury. By this method of isolation any possibility of a transferred infection from the first native snails was eliminated.

It was found that several hundred young snails (up to 15 mm. shell length) could be raised in the small three liter jars, with no excessive overcrowding effect. Very little pre-hatching mortality was observed. Baily (1939) noted very high infant mortality in his cultures. As the snails increased in size the smaller undesirable individuals were removed, providing those remaining with an increasing volume of water per snail. Maximum growth for the larger snails was obtained with a density of about twenty snails per ten liters of water, or six in each three liter jar. Under these conditions the largest snail reared attained the shell length of 62.5 mm., and many others reached lengths between 55 and 60 mm. In some instances aquaria with two to three times the optimum number were carried through. In these the individual growth of the snails was quite variable, only a few being able to reach maximum size in the usual time. On the whole, *L. s. appressa* cultured as described in this paper attain demonstrably greater size than their wild parents. Baily (1939) found this to be true also for *L. columella*. F. C. Baker (1928) gives 53 mm, as the measurement of the longest snail recorded in that publication. Hogg (1854) writes that British shells of *L. stagnalis* measure 47 mm. in length. Crabb (1929) stated that under optimum culture conditions he reared *L. stagnalis appressa* (172 days old) 44 mm. in length.

Notes on Life History in the Laboratory

The original stock of *L. s. appressa* used in this study was collected by Dr. Sterling Brackett in the summer of 1939 in Fox Lake, Dodge County, Wisconsin. The snails were found in dense little aggregations near the mouth of a sluggish stream, feeding in thick growths of aquatic vegetation. These animals are said to live about one year in their natural environment, although there is little information available as to how they survive the winter months. The adults lay eggs in the latter part of the summer. The eggs apparently hatch in the fall and the newly hatched snails presumably survive the winter, resume growth and reach sexual maturity by the end of the summer. With the onset of cold weather the adults probably die. This fragmentary story is one

pieced together from the few available facts on the life cycle of this snail in its natural state.

By the methods described opportunities were provided for the daily observation of the habits and life cycle of *L. s. appressa* cultured in the laboratory. The snail is not as slow-moving as is proverbially proclaimed: it "glides" across a smooth submerged surface in its more active periods at the rate of 7.5 cm. per minute, or 4.5 meters per hour! There are very few if any pedal contractions in this movement: the animal slides over glass in an apparently effortless advance, propelled, it seems, almost entirely by the ciliary activity of the under side of the foot. The shell, held gracefully over the rear part of the body, is at times allowed to lag behind the progress of the foot, and is then drawn up again, simulating the mode of progression of a land snail. Much of the time the shell is moved from side to side, sometimes leisurely, sometimes quite violently if the snail is strongly stimulated. The tentacles are generally held forward and slightly upward from the head, being contracted to about one third the length when the snail is irritated; they are merely waved or twitched slightly in normal behavior. A continuous regular movement of the mouth parts is commonly observed as the snail glides along, the radula rasping at the substratum as the snail advances, whether food is present or not. When harder foods such as bits of the stem of lettuce are consumed, the velar lips are used in clasping the food as rasping occurs. Some snails have been seen to wrap the foot completely about small floating pieces of lettuce as they were eaten; floating snails have been seen to bend the lateral portions of the foot into a trough which facilitated the holding of bits of mucus and fecal pellets. It was occasionally observed that one snail, rasping continuously, would advance over the rear portion of another snail's foot. This frequently caused the second snail to contract the irritated foot with a violent movement.

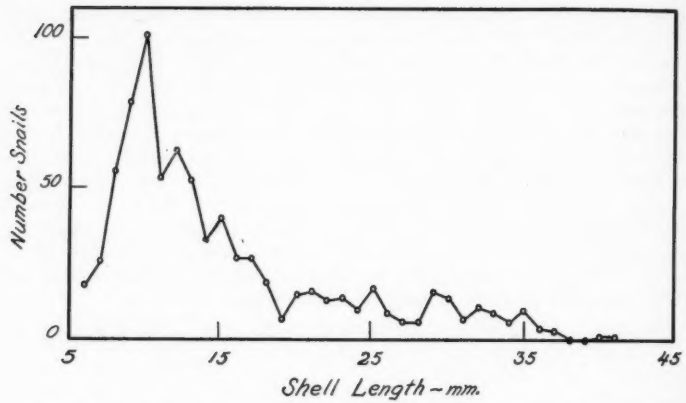
Food ingested by this pulmonate is retained in the alimentary tract about two hours. The feces are voided very slowly (several minutes for the extrusion of a few mm. of feces) in cylindrical, compact pieces one to two cm. long. The color of the excrement depends on the type of food eaten, but is usually of a dark muddy brown color.

The required oxygen is obtained through both cutaneous and pulmonary respiration. The respiratory chamber is a closed off portion of the mantle cavity which is abundantly supplied with blood vessels and opens under the right central part of the shell through fleshy pneumatoporal lips. When the snail reaches the surface of the water the pneumatoporal lips slowly relax and open, revealing the deep lung within, extending across the dorsal inner half of the body whorl. The pneumatoporal lips are thickly coated with a mucus-like substance of almost greasy consistency, which prevents the water from flowing into the respiratory chamber. If the level of the water is raised about a snail which has opened the pneumatopore, in such a way that the strain on the meniscus of the water around the pore is increased, the pore is closed quickly. Conversely, if the water level in a tank is lowered gradually, each snail in turn, as soon as it senses the meniscus on its fleshy parts, turns to the left, exposes the pneumatopore on its right side and opens it to the air. The pneumatopore opens with an audible smack; at summer temperature when metabolic activity is high, the snails in a quiet laboratory can produce quite an

audible proof of their presence. Snails expel air from the pneumatopore as it opens, as noted by prominent distension and bursting of the film of mucus which catches across the pneumatoporal opening. When a snail descends into deep water, the respiratory chamber is full of air, making the snail quite buoyant. Thus snails on the bottom of tanks often become dislodged from the loose detritus and float rapidly to the surface. Sometimes, too, especially if the snail is disturbed, sufficient air is forced from the lung by sudden contraction to permit the snail to sink quickly to the bottom. This may be a protective measure in the natural state since it allows snails to sink out of the reach of terrestrial predators. At periodic intervals, shorter in warm weather than cold, snails crawl to the surface to renew their partially depleted air supply. Movements concerned with respiration are discussed at some length by Dawson (1911) and Walter (1906), and are similar to those noted here.

Much has been written in the literature about snails creeping through the water on invisible slime strands (Frömming, 1929, and others). *L. s. appressa* is too large a snail to do this as effectively as do the small and active *Physa* (Dawson, 1911), or *L. elodes* (Walter, 1906). Our *Lymnaea* have often been observed to hang suspended in midwater by an invisble mucus strand. In this position the head presents a curious "moose-like" appearance with its soft parts extended their fullest length seeking a "foot hold."

Overcrowding of growing snails has a decidedly detrimental effect on extent and rate of growth, the number of snails that reach optimum size, condition of the shell, etc. Overcrowding has been discussed at some length by Colton (1908), Turner (1927), Goetsch (1928), Crabb (1929), Forbes and Crampton (1942b) and others. To obtain quantitative information on this factor, 50 normal generation III laboratory egg masses (2,589 total eggs; average of 52 eggs per egg mass) oviposited during a five day period, were suspended in 10 liters of well aerated water in a clear glass aquarium. All hatching occurred from the 15th to the 28th day. The experiment was run for 200 days under normal feeding conditions at room temperature; water was changed infrequently. Pre-hatching mortality was negligible. At the end of this period, when the larger snails were already ovipositing, the snails were all counted and measured: 791 snails survived (30.5% survival). Of all the snails that died prior to the count mentioned all were under 10 mm. shell length at time of death, with the exception of three which died from accidental breakage of the spire (lengths: 25, 30, and 33 mm.). The shells of both living and dead snails presented a heavily mottled, eroded periostracum; otherwise, the living snails seemed normal. The range of shell length of the living snails is presented in Graph 1. The mode of the curve falls at 10 mm. In spite of extreme crowding, 136 snails attained lengths in the range 20-30 mm., and 52 in the range 31-41 mm. As shown by the following experiment and also by previous investigators, the stunted condition caused by overcrowding appears to be only temporary. Twenty-five of the smallest snails from the previous experiment, 6-7 mm. long, were placed in a 10 liter tank under normal conditions. In 70 days the surviving 18 snails had attained the following lengths: 20 mm.—1 snail; 29-1; 32-2; 33-1; 34-2; 35-5; 36-1; 37-3; and 40-2. New shell growth added in the second experiment was uniform and healthy.



Graph 1.—Shell length variation of 791, 200 day old *L. stagnalis appressa*, cultured in 10 liters of water.

In this laboratory the snail's maximum span of life has been about fourteen months. Considerable disagreement exists in the literature as to the normal length of life of lymnaeids. An oft quoted statesment of F. C. Baker (1911) has engendered much comment: "The duration of life in the family Lymnaeidae is from three to four years, full maturing being reached in about two years." Boycott (1936) writes that all the pulmonates, in Britain at least, are annuals with a natural duration of life of nine to fifteen months or less, except *Planorbis corneus* which lives and goes on growing for two or three years and breeds correspondingly often; that *L. peregra* in hot summers may get through two generations in one season; and that wild *L. truncatula* in Wales normally have two or even three generations in a summer, which may explain why the largest specimens are found early in the spring. In this country Crabb (1929) found that few *L. stagnalis appressa* lived longer than nine months when kept in solitary culture in the laboratory. The Winsors (1935) found that only a few snails lived over seven months in the laboratory. Baily (1939) kept his snails living between seven and eight months in the laboratory. Olsen (1944) observed that the lymnaeid snail, *Stagnicola bulimoides techella,* in its native Texan habitats follows a rather well-defined pattern with two generations annually, one in midwinter and the other late in the spring. The snails surviving summer drought are predominantly juveniles. The adult snails usually die when about six months old; but in the laboratory lived as long as twenty-five and a half months. Forbes and Crampton (1942a) found that *L. palustris* seldom lived over eight to ten months in the laboratory. Seshaiya (1927) believes that the minimum duration of life of *L. luteola* under natural conditions is probably three years.

In *L. s. appressa* after sexual maturity is reached reproduction continues almost unabated until the end of the life cycle. The death of the animal in the laboratory was apparently not caused by predators, parasites or other

causes found in the environment, but appeared to be the result of a slow exhaustion. Autopsy of senescent snails invariably discloses a badly atrophied liver and the remaining organs, with the exception of the reproductive organs, are badly emaciated. The reproductive organs remain large, full and seem normal. In snails, kept in solitary culture throughout their sexually mature existence and observed for egg laying, oviposition continued up to about one or two weeks before the death of the animal, and the life cycle appears shorter than that of snails in mass cultures.

In the laboratory sexual maturity (laying of the first egg mass) in our snail is usually reached within a little less than three months in the summer and up to four months in the winter, dated from the time of oviposition. In *L. columella* (Baily, 1939) reared singly in separate containers, snails in one race started oviposition at the age of about two months, and in the second race in about two and a half months. Crabb (1927a) relates that of fifty-four *L. stagnalis appressa* from the same egg mass, seven laid their first egg masses about two months after hatching (this would be approximately two and a half months if dated from the time of oviposition). In 1929 Crabb reported the ages of several snails at laying times as ranging from two and a half to four months. Colton (1912) reports that the interval from hatching to egg laying for thirteen *L. columella* was one to three months (calculated from time of oviposition, this would be approximately one and a half to three and a half months). In this species the Winsors (1935) observed that egg laying usually commenced at about two and a half months.

In *L. s. appressa* copulation begins shortly before the onset of oviposition. The snail is sexually monoecious. Any snail may act as "male" or as "female" in copulation. There are no indications that any snail of this variety remains exclusively "male" or "female." Several snails were kept in solitary culture throughout their sexually mature existence except that at weekly intervals they were placed with other snails for a few hours under observation to permit copulation. Close watching indicated that there was no constant tendency for "maleness" or "femaleness"; it would seem that it is the first snail which is able to assume the "male" position, that acts as "male." F. C. Baker (1911) describes in detail the act of coitus in some lymnaeids.

In the early stages of mating the "male" snail succeeds in adhering to the shell of the "female," and glides over the main body whorl towards the female genital pore, everting the preputium as it advances. This organ then commences a series of searching movements which continue until the penis is inserted in the female genital pore of the "female" snail. Young snails have more difficulty and require longer to locate the pore than older snails; an hour or more may lapse before it is found. During the act of coitus, the "male" foot is strongly appressed to the right side of the body whorl of the "female," and the preputium and penis of the "male" are extended in an arc over the edge of the shell of the "female" to the female pore (Fig. 1). An extra quantity of mucus is secreted by the ventral surface of the foot of the "male" during coitus which serves to bind the two animals together more strongly. So strongly is this adherence that it is difficult to separate them without injury to the "male." The penis may remain inserted in the female genital pore for three or four hours. If the "female" assumes the role of "male" directly after

the first copulation, and this happens occasionally, then the total time of copulation may be doubled. Once the penis is inserted in the female pore it is seldom withdrawn until copulation is complete. During copulation the white vas deferens of the "male" is visible undulating within the cavity of the everted preputium.

Confirming the observations of Crabb (1927a) we have noted as many as three snails copulating together at once, the two end snails acting one as male, the other as female, and the middle one as both.

In some instances snails kept in solitary culture were observed attempting what appeared to be autocopulation, the penis being extended to the female

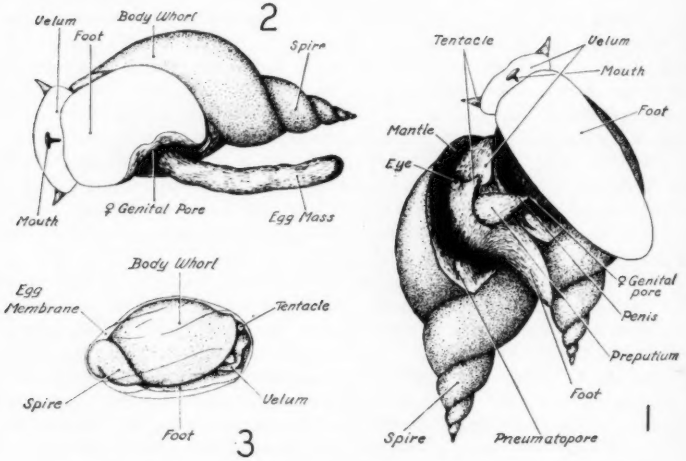


Fig. 1.—A pair of *L. s. appressa* copulating. The "female" is gliding over a glass surface.

Fig. 2.—A *L. s. appressa* depositing an egg mass; observed as the snail glides over a glass surface, appressing the egg mass to the glass substratum.

Fig. 3.—A young *L. s. appressa* a few hours before hatching, shown in its thin wrinkled egg membrane.

genital pore. Whether actual flow of sperm occurred could not be observed, but this indicates that self-impregnation may possibly occur in this manner. Crabb (1927a) never observed "self-copulation" himself, but cites others who did. In 1928 he cites observers who recorded that two snails, feet together, anterior ends reversed, were copulating reciprocally. Colton (1918) stated that self-copulation has been observed.

During the mating period snails are very sensitive to mechanical stimulation such as jarring of the containers. As soon as two snails previously kept in solitary culture are placed in the same container one of them or both become active and start searching for the other snail. In this state they may evert the

preputium repeatedly before actual contact is made with the other snail. In one instance a string of sloughed-off epidermal material from around the base of the mantle of one snail was reached by a second. The preputium was everted and brought in contact with the epidermal string. On another occasion a snail that was crawling on the aluminum strip of one of the floating feeders was seen to pass its penis along and under the edge of the metal, with much the same type of movement used in seeking the female genital pore.

One of the research assistants in this department on one occasion observed a snail ejecting sperm into the water. This was collected with a pipette and definitely identified. Colton (1908) noted that one lymnaeid expelled sperm after copulation with a second species.

Copulation occurs most commonly in a tank of snails when the food supply has been recently depleted. Under such conditions practically every snail in the tank may be copulating, and mating is not limited to pairs of snails but may include three or four animals in one cluster. Crabb (1927b) noticed that egg laying in this subspecies occurs with equal frequency in the night and day.

Fertilization is internal. The oval eggs are contained in a subcylindrical gelatinous matrix which together with the eggs is termed the egg mass. These masses vary considerably in length and width and in the number of eggs contained. Masses from the average adult snail of 45 mm. shell length average 45 mm. in length, 3 mm. in width and 2 mm. in depth. Such an egg mass encloses about 100 eggs. Egg masses as short as 15 mm. and some over 60 mm. have been measured. A sample count of 169 average egg masses gave 9,816 eggs and 5,221 mm. of egg masses. This is an average of 58 eggs per mass and 1.88 eggs per millimeter length of egg mass. Variability in the number of eggs per unit length of egg mass is due in part at least to (1) rate at which snail glides and extent of turning during oviposition, (2) diameter of lumen of reproductive canal which increases with growth of the snail and (3) speed of passage of eggs into the canal. The eggs, especially if there are more than two or three longitudinal rows within the egg mass, are placed peripherally, leaving a space of gelatinous material down the center of the mass. Only one embryo is generally found in a single egg. However as many as four have been seen in some eggs. The majority of these polyembryonic eggs are placed in that end of the egg mass which comes out of the genital tract last and consequently is deposited last on the substratum. None of these embryos have ever been observed to develop to the hatching stage. Once two such embryos were seen to grow to the fully shelled stage, but did not hatch. The polyembryonic condition (or polyvitelliny) in *L. s. appressa* has been studied in some detail by Crabb (1927b, 1931). He states that thirty-five instances are recorded in which each egg had had fifteen to forty-six vitelli. Twenty snails laid 19,863 eggs, 273 of which were polyvitelline. This same condition has been studied in *L. columella* by the Winsors (1932).

When depositing an egg mass a snail indents the right side of the foot directly under the female genital pore. A groove is thus formed by the invaginated margins of the foot and extends up to the pore. As the mass passes out of the vagina it slips down the groove and hits the substratum at an acute

angle. Simultaneously the snail glides slowly forward, so that the egg mass is actually secured to the substratum at the rate at which the snail is creeping forward, a pace considerably slower than the normal one. The ovipositing snail holds its shell and mantle closely down against the sticky egg mass thus pressing it against the substratum and effecting thorough affixation (Fig. 2). That portion of the mesopodium immediately below the genital atrium, lying in the way of the emerging egg mass, is contracted and folded back out of the way. The snail in its slow forward progress, in many cases, continues feeding over the substratum. As the egg mass is passed, the foot contracts more and more into itself as if exerting pressure upon the egg mass. At room temperature it takes an adult snail about twenty-four minutes to pass a 35 mm. egg mass. Soon after the egg case is oviposited, the snail proceeds upwards to the surface of the water. The definitive shape of the egg mass after deposition depends upon the straightness of the snail's forward course. The newly laid mass bears a semitranslucent milky outer case with marked longitudinal striations. The inner fluid and egg membranes are colorless. A few hours after oviposition the egg mass clears completely and the eggs, containing the highly granular yellow embryos, become clearly visible. In the laboratory aquaria the majority of the egg masses are deposited in an area about six inches below the surface of the water. However, masses are not infrequently found on the shells of other snails, on lettuce, on food floats, etc. Again, there is a tendency for masses to be affixed to surfaces away from the light and to surfaces of darker coloring. Egg laying continues throughout the year. The most prolific production occurred in the late summer and early fall months and the minimum laying took place in the late spring and early summer. Nekrasov (1927, 1928) holds that the form of the ootheca, number and form of the eggs, and the structural peculiarities of the egg masses are characters which should be considered in the classification of snails. In his classification the egg masses of this snail are described as "capsula vera, gibbosa."

Egg laying may be approximately doubled by the addition of cooked wheat cereal to the normal lettuce diet. In one experiment 15 sexually mature, generation II laboratory snails were placed in 10 liters of water in each of three glass battery jars (a total of 45 snails). All tanks were provided with an abundance of lettuce, a pinch of nutrient salts, and a little sand was added to each tank every time the water was changed. Even though water was changed weekly or bimonthly, a dense growth of attached and floating microscopic forms, mostly algae, was present much of the time. In addition to the above, Tank I was provided with a continuous supply of cooked wheat cereal on floaters, Tank II with a continuous supply of strips of dried raw beef liver on floaters, and Tank III was used as a control. This feeding arrangement was maintained for 169 days; at the end of this period, the diets were reversed as follows: Tank I was used as a control and Tanks II and III were given cream of wheat. The liver was discontinued in Tank II. The results are given in Table 2.

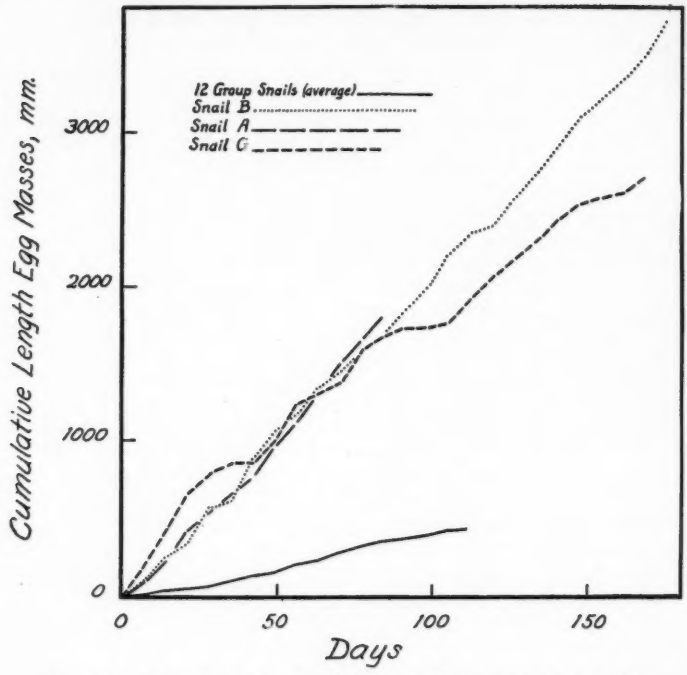
The data listed under the initial diets as for 29 days were taken from the last 29 days of the 169 day period as a comparison for the data in the second part of the experiment. As shown in the table under "Diets after reversal," discontinuation of the wheat cereal in the diet decreased egg production; and

TABLE 2.—Egg Masses Laid Under Different Diets.

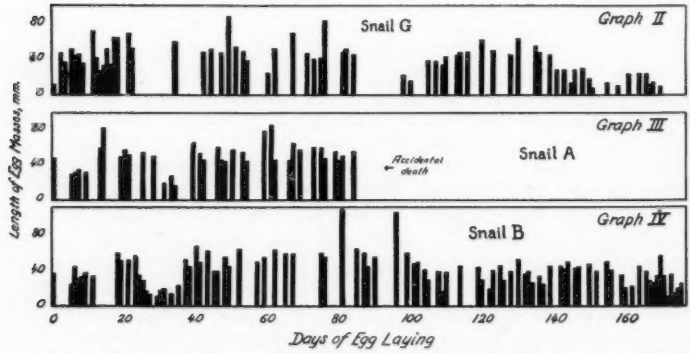
Culture No.	I	II	III
Initial Diets	Wheat	Liver	Lettuce only
Total numbers (169 days)	408	198	288
Total length (29 days)	3126	1351	1334
Average length (29 days)	37.1	31.7	26.9
Maximum length (29 days)	61	45	37
Diets after reversal	Lettuce only	Wheat	Wheat
Total number (29 days)	76	61	91
Total length (29 days)	2279	1945	2532
Average length (29 days)	30.7	33.3	27.7
Maximum length (29 days)	50	53	48

conversely, addition of wheat cereal to a diet previously lacking it, boosted egg production. A liver diet seemed to favor egg production slightly.

To observe the frequency of egg laying in a single *L. s. appressa* (and thus a non-copulating one) and to correlate oviposition with shell length, a 17 mm. snail, designated as G, was kept in solitary culture throughout its sexually mature life in three liters of water in a glass aquarium. Optimum aeration, abundant food (lettuce and wheat cereal) and sand were provided continuously. Water was kept clean. Snail G did not start ovipositing until 115 days old (from the time of hatching), shell length 51 mm., and continued to oviposit (see Graph 2) until it reached the age of 286 days. The total length of egg laying period was 171 days, or 60% of the life span. During the 171 days of oviposition, egg masses were actually deposited on only 45 days (26%). A total of 68 egg masses (2,696 mm. of egg masses, and roughly 5,000 eggs) were laid in the life span of the snail. The average length of egg mass was 39 mm., the shortest egg mass measured 8 mm. and the longest 72 mm. Frequency of egg laying is indicated in Graphs 1a and 2. The experiment was repeated with two of the first generation offspring, A and B, also kept in solitary culture and thus non-copulating. Table 3 and Graphs 2, 3, and 4 present a comparison of the results. Snail G and offspring B appeared to die the usual death in which all the internal organs except the reproductive were badly atrophied. Offspring A had its spire tip broken which caused premature death about five days after the injury. The snails oviposited almost to the day of death. Oviposition occurred at a slightly irregular rate interrupted by short periods of irregular duration. The maximum length of egg masses per day increased sharply shortly after egg laying commenced, reached a peak somewhere in the middle of the egg laying period and then gradually tapered at the end.



Graph 1a.—Comparison of egg production in isolated non-copulating and in group copulating *L. s. appressa*.



Graphs 2, 3 and 4.—Comparison of frequency and quantity of egg mass production in isolated non-copulating *L. s. appressa* (Snail G) and first generation offspring (Snails B and A) through the total egg laying period.

TABLE 3.—A Comparison of Egg Production in Isolated Non-copulating and Group Copulating *L. s. appressa*.

	Snail G	Snail A	Snail B	Group of 12 snails (average per snail)
Total period of egg laying, in days	171	85	177	106
Number of actual days in which egg masses were deposited	45	37	90	.....
Per cent days egg masses deposited	26	43	51	.....
Total length of egg masses deposited, in mm.	2696	1874	3785	470
Total number of egg masses deposited	68	42	93	13.8
Total number of eggs laid	5000	3500	7100	880
Average number of eggs laid per day	30	41	40	8
Average length of egg masses, in mm.	39.0	43.7	40.7	33.7
Shortest egg mass, in mm.	8	17	11	7
Longest egg mass, in mm.	72	65	65	54
Length of shell at start of oviposition	51	47	40	34.8 (34–37)
Length of shell at cessation of oviposition (and death), in mm.	56	51	49	50.4 (48–54)

To determine the effect of copulation on the extent and rate of oviposition of a group of snails living together constantly, twelve *L. s. appressa* (each 25 mm. long) were isolated in a glass jar containing ten liters of water. This experiment was run concurrently with that of Snail G and with snails of the same laboratory generation. Optimum aeration, abundant food (lettuce and wheat cereal) and sand were provided continuously. Water was changed weekly and the individual snails were marked with India ink painted over with household cement. Egg masses started appearing in the tank when the average shell length of the snails reached 34.8 mm. (see column four of Table 3), decidedly smaller snails than the non-copulating ones when oviposition began. The egg masses laid by the twelve snails were collected every seven days, and the average cumulative weekly length of egg masses per snail is so indicated in Graph Ia, along with similarly computed data for the non-copulating snails. This experiment (and that of Snail G) was started in February and for convenience was run only 106 days. As indicated by Table 3 and Graph Ia, an astonishing difference in the productivity of eggs, as yet

unexplained, occurred between copulating snails living together continuously and individually isolated non-copulating snails. Relatively more crowding or the effect of copulation in the group snails are possible influential factors.

A comparison of the data in Table 3 with that found in the results of other investigators discloses some interesting correlations and some disagreement. The Winsors (1935), in agreement with our findings, noted that isolated snails (*L. columella*) laid more eggs than paired snails. Contrary to our findings, they discovered that single snails laid at least as early as pairs. Crabb (1927a), contrary to our observations and those of the Winsors, states that individual *L. s. appressa* isolated "in ovo" laid the same number of eggs, on the average, as individuals in mass cultures. Boycott et al. (1930) for *L. peregra* agree with our data in *L. s. appressa* stating that in the case of animals in solitary culture egg production begins markedly later than in paired snails. Seshaiya (1927) writes that an individual *L. luteola* laid eggs once each two days, the number in the successive egg masses alternately rising and falling: as the number of egg masses laid by an individual increased, the number of eggs per egg mass tended to decrease.

As regards the egg production of individual snails, the following comparative data are available, usually for the best laying snails. *L. s. appressa* (Crabb, 1927a) laid seventy egg masses (80,100 eggs each) in 195 days, or as calculated: approximately 6300 total eggs, or 32 eggs per snail per day. *L. stagnalis* (Popovici-Baznosanu, 1928) laid 2094 eggs in 22 days or 95 eggs per snail per day; the author does not say, however, whether the days given are for the total laying period, or the actual days in which egg masses were deposited. *L. columella* (Baily, 1939) in one race laid 2735 eggs in 90 days, or 30 eggs per snail per day; and in a second race, 3727 eggs in 115 days, or 32 eggs per snail per day. In another *L. columella* (the Winsors, 1935) egg production varied from 1.94 eggs per snail day (for the densest populations: seven snails) to 17.12 eggs per snail day (for single snail). *L. luteola* (Seshaiya, 1927) laid 1650 eggs per year, or approximately 4.5 eggs per snail per day. *Stagnicola bulimoides techella* (Olsen, 1944) laid 6479 eggs in 129 days, or about 50 eggs per snail per day.

The rate of embryological development of *L. s. appressa* is strongly influenced by oxygen concentration and is largely a function of the temperature. Insufficiently aerated egg masses do not hatch. Being curious to observe the exact effect of temperature on the rate of heart beat of unhatched snails, we isolated an egg containing one normal, fully developed, unhatched snail (1.3 mm. long) in a Stender dish and subjected it to temperatures in the range of 36-100° F., four minutes at each temperature. The resulting curve was distinctly sigmoid. At 36° F. the heart beat was 8; at 72° F., 73; and at 100° F., 126. Our observations on embryological growth have been made at room temperature.

Because of the high opacity of the outer member of the egg mass when first oviposited, the first stages of the embryo were observed in eggs removed from the egg mass. In five out of fifty eggs masses examined at one time, the last few eggs contained double or triple, distinct and separate embryos. This polyembryonic state has been noted only in eggs located in the region of the egg mass which is oviposited last. The anterior end, or end to appear first in

oviposition, is rounded and blunt, while the posterior end narrows to a tapering cylinder which breaks off abruptly. The largest number of eggs to be recorded in any egg mass to date is 123.

When first laid the fertilized ova are uncleaved and appear to possess but one extruded polar body and measure approximately 120 to 150μ. In about four hours first cleavage is complete and two polar bodies are visible. Second cleavage is complete in some nine hours. In eighteen hours the embryo is roughly at the sixty-four cell stage (140μ long). In approximately 100 hours the embryo has reached the trochophore stage and is rotating energetically (about 200μ long). In six days the veliger is in the neighborhood of 500μ and begins to show definitive external form in the head, shell and foot. By the ninth day some movement is observed in the foot, and by the eleventh day the animal (shell length about 800μ) is definitely creeping on the inner surfaces of the egg membrane. Development within the egg is pronouncedly uneven so that at room temperature snails hatch in about fourteen to eighteen days. About four days before the snails start hatching from the eggs and emerging into the egg mass they begin rasping on the inner surface of the egg. The pneumatopore remains open during the snail's prehatching phase, offering free passage of fluids between the lung and the egg lumen. The time relation of the larval development of *L. japonica* (Imai, 1937) at 18° C. seems similar to that of this snail at 20° C.

The fully formed snail within the egg continues growth until it amply fills the egg cavity. During its later prehatching stages it has been creeping over and rasping off the inner surface of the egg case. Thus by the time the animal fills the egg membrane, the membrane has been reduced to a very thin envelope through which the contours of the young snail shell and foot protrude. At this time the egg closely resembles a much wrinkled, transparent, cellophane capsule (Fig. 3). Rasping is continued until the membrane is rasped through at some point, allowing the snail to escape into the cavity of the ootheca. This cavity is also filled with a gelatinous substance which during the prehatching stages of the snail is of a viscous, jellied nature holding the eggs in place, and which, after hatching commences, turns to a more fluid consistency. Snails tend to congregate at the ends of the ootheca where they continue rasping. Through the unified efforts of many young snails an opening is eventually scraped through the oothecal covering and the snails pass out into the water. The egg and the egg mass serve the dual purpose of providing a source of nutrition and protection; this is in marked contrast to marine free-swimming snail larvae which go uncovered and obtain their food in the plankton of which they form a fraction. Once in the lumen of the egg mass, the snails gather under the surface of the ootheca opposite the surface of affixation before moving to the ends. In a detached egg mass snails were observed to seek the upper surfaces (already displaying their negative geotropism) whether site of affixation or not.

At the time of hatching from the egg, snails measure about 1.3 mm. in length (egg is about 1.6 mm. long). Their rate of hatching is very irregular. In one egg mass of 123 eggs the following order of hatching was noted: On the first day ten snails hatched; on the second, eleven snails; by the fifth, sixty-one; on the sixth, five. On the following day, seven days after the first

hatching, five snails (about 1.7 mm. long) escaped from the ootheca. The actual escaping period for snails from any egg mass, after the first snail has escaped, seems to extend through about eight days.

The immediate posthatching behavior of newly hatched snails can be observed on an inverted watch glass placed in a Petri dish partly filled with water. Once out of the egg mass the snail continues to exhibit its negatively geotropic tendencies and moves upwards to the surface of the water. Under the surface film it has considerable difficulty overcoming the strong surface tension. It continues its efforts until it is able to force the pneumatopore above the film. Then its contortions are increased in its attempt to fill the lung with air. The struggle ceases when the shell has been swung around to such a position that the lung fluid can drain out. With a lung full of air the pulmonate returns to the water and continues its interrupted feeding, a true "air breather."

A large percentage of snails only a few weeks old, and a few days out of the ootheca (the age of a snail is best designated from the time of oviposition), have the curious and frequently suicidal behavior of creeping up out of the water onto the sides of their container and remaining there to dry out upon the substratum. Many seem unable to return to the water and die of desiccation. No good explanation has been arrived at for this phenomenon. This peculiar habit has also been observed in *L. columella* (Colton, 1908; the Winsors, 1935; and Baily, 1939) and in *L. elodes* (Walter, 1906). It may possibly have some connection with the instinct of freeing the respiratory chamber of fluid. At any rate, it is a behavior which causes considerable loss of young snails in the nurseries. Whether it occurs in the natural environment is not known. One means of reducing mortality under these circumstances is to bring the water level in the jar very near the glass cover, and to increase the bubbling of air in the nursery tanks so that the inner surfaces of the tank above the water are kept well moistened.

A few small tests of the ability of young snails to withstand exposure to air were conducted. Snails were placed under varying conditions of humidity and at intervals sample snails returned to water. Those displaying activity within an hour and feeding in another hour or so were said to recover. Five to eight-millimeter snails recovered completely after three days exposure to room air at room temperature, and some recovered even after fifteen days exposure. If the aperture was well covered with a film of mucus, as often occurred, they could survive an even longer period out of the water. Twenty-millimeter snails withstood as much as eight days out of water at room temperature in the humidity afforded by a closed dry Petri dish. At lower temperatures, resistance to exposure was greater. Zhadin (1926) found that *L. palustris* remained alive a month in a $CaCl_2$ desiccator. Pilsbry (1896) records a *L. bulimoides* which survived forty-five days out of water. Kolpakov (1929) found that lymnaeids in nature survive in drying ponds by burying themselves in the mud or in decaying vegetable matter, or by secreting a protective mucous layer over the aperture. Cawston (1929) found that certain lymnaeids survived as long as sixty days buried in soil. And Barlow (1933) noted that *Bullinus* and *Planorbis* survived thirty to fifty days in drying canal mud. As regards temperature resistance Baker (1911) writes that lymnaeids have been frozen in solid ice

and survived; and have been observed crawling under solid ice in ponds. Weigmann (1936) found that *L. stagnalis* subjected to low water temperatures, died from freezing at about –1.5° C.; but that they could be supercooled to –3.5 to –4.5° C. without freezing and subsequent death. The ability of these snails to withstand partial drying was utilized one summer in successfully shipping some of them a thousand miles in drained, water-soaked agar agar. Barlow (1933) employed the ability of *Bullinus* and *Planorbis* to withstand some desiccation by transporting them through the post from Egypt to the United States. And Kolpakov (1929) sent *L. stagnalis* and *L. palustris* and other species in dry postal packages from Saratov to Tashkent and return.

L. s. appressa have been observed to reach sexual maturity in slightly less than three months. The oldest snails raised in the laboratory reached the age of approximately fourteen months. The longest snail raised measured 62.5 mm. in length; and the heaviest snail ever noted, weighed 11.6 gm. and was 53 mm. long and 32 mm. in diameter. A snail measuring 48 by 26 mm. averages about 7 gm. wet weight, though some specimens considerably exceed this.

Conclusions

Snails raised by the method here described seem "normal," insofar as can be determined, even after twenty generations of laboratory culture. They attain greater size than their wild progenitors (Baker, 1928), and as far as can be ascertained from the literature, are larger than the largest snails of the same subspecies cultured by other investigators. The time required for these snails to attain sexual maturity in this laboratory compares favorably with that for the same and closely related species recorded by other workers (Baily, 1939; Crabb, 1927a, 1929; Colton, 1912; the Winsors, 1935), and the life span in this laboratory is longer than that recorded for the same subspecies (Crabb, 1929), for *L. columella* (the Winsors, 1935; Baily, 1939), and for *L. palustris* (Forbes and Crampton, 1942a) under laboratory culture conditions. As regards egg production in snails kept in solitary culture, for which there are some limited though perhaps not very significant comparative data available, the best snails in this laboratory laid somewhat more than *L. s. appressa* of Crabb (1927a) and *L. columella* (Baily, 1939), and significantly more than *L. columella* (the Winsors, 1935) and *L. luteola* (Seshaiya, 1927).

Summary

1. A simple inexpensive method is described for culturing *L. s. appressa* in large numbers in relatively small space through an indefinite number of generations. This method involves rearing the snails in three to ten liters of aerated water in deep covered glass jars located in subdued natural light, with approximately two adult snails to each liter of water. The water used is deep well water rich in calcium and magnesium and alkaline in reaction. The jars are cleaned and the water changed weekly, or bimonthly at the longest, and in winter the cold water is warmed to the prior temperature of the aquarium before the snails are placed in it. A small quantity of fine sand, used in trituration of food by the snail gizzard, is furnished in the aquaria. Loose green

head lettuce leaves are kept available in the aquaria most of the time; and weekly, wheat cereal cooked in milk and supplemented by a mixture of balanced salts is added.

2. Prehatching mortality by this method is negligible. Sexual maturity is reached in about three months and the average final length of snails reached is between fifty and fifty-five mm. The longest snail ever cultured attained a length of 62.5 mm. The maximum life span of the snail under these cultural conditions is fourteen months.

3. Observations on crawling and feeding, movements concerned with respiration, overcrowding, copulation, oviposition and egg production, gross embryology, hatching, exchange of water for air in the lung, desiccation, etc., are recorded.

4. Egg production was approximately doubled by the addition of cooked wheat cereal to the normal lettuce diet. Non-copulating snails, kept in solitary culture through their sexually mature existence, laid a greater number of eggs per snail than copulating snails living in a group. Snails kept in group culture started ovipositing sooner than in solitary culture. In individual snails the maximum length of egg masses per day increased sharply shortly after egg laying commenced, reached a peak somewhere in the middle of the egg laying period and then gradually tapered at the end. Oviposition in snails kept in solitary culture occurred in periods of variable duration alternating with rest periods.

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Incidence of Worm Parasites in Minnesota Mustelidae and Host Lists and Keys to North American Species[1]

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Introduction

The parasitological examination of various species of wild North American Mustelidae, until recently, has been limited to a few animals or has been incidental to other investigations such as food habit studies. Much of the information pertaining to this group of host species has resulted from the investigations carried on in the interest of fur farmers. Some additional parasitological data have been obtained by the examination of animals which have died in zoological gardens. The present report is based on the necropsy findings for 547 mustelids of eight species. The known helminth parasites of North American Mustelidae are listed under their hosts, and keys for their determination are appended.

Stiles and Baker (1935) "Catalogue of Parasites Reported for Carnivora (cats, dogs, bears, etc.)" listed the known parasites of mustelid mammals with the literature pertaining to them. Their manuscript was submitted for publication August 26, 1931. For this reason, a review of the literature of helminths of North American Mustelidae must go back to about 1930.

Review of Literature

Helminths of Mink.—Bosma (1931, 1934) described the trematode, *Alaria mustelae*, and elucidated its life history. Ameel (1931, 1934) reviewed the life history and distribution of *Paragonimus*, and Wallace (1931) also discussed the occurrence of this species. Hanson (1932) gave an annotated list of mink parasites which included *Trichinella spiralis*, *Filaroides mustelarum* (=*martis*), *Dioctophyme* (=*Dioctophyma*) *renale*, and *Gnathostoma spinigerum*. The record of *T. spiralis* is the only one for the mink in North America. In 1932, Chitwood reported the Guinea worm, *Dracunculus medinensis*, from a mink taken in Nebraska.

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Law and Kennedy (1932) listed nine species of helminths recovered from mink in Ontario. Price (1932) recorded the first occurrence of the fluke, *Euparyphium inerme,* in North America. In 1932, Skinker collected the roundworm, *Molineus patens,* from mink in Mississippi, and in 1935, she redescribed *Taenia tenuicollis* and its larva, *Cysticercus talpae,* from the mink and muskrat respectively.

Sprehn (1932) described a new species of fluke, *Alaria freundi,* and a new species of roundworm, *Molineus americanus,* from mink newly imported into Germany from America. *M. americanus,* according to Leiper (1936) is a synonym of *M. patens,* and Travassos (1937) tentatively agrees in his monograph on the Trichostrongylidae. Allen's 1934 list of parasites of fur-bearing animals contains, with a few additions, the same information as the earlier list of Law and Kennedy. Wallace (1935) described the trematode, *Sellacotyle mustelae,* from mink in Minnesota and elucidated its life history. In 1936, McIntosh reported the trematode, *Euryhelmis squamula,* from minks taken in Minnesota and Maryland. The metacercaria of this species was recovered from the frog, *Rana pipiens,* in Virginia. La Rue and Ameel (1937) reviewed the life history and distribution of the lung fluke, *Paragonimus.*

Groves (1937) examined wild minks in Wisconsin that had died from the effects of *Dioctophyma renale,* the giant kidney worm, and from *Paragonimus.* Woodhead and McNeil (1939) reported that 8.6 per cent of the wild minks that they examined in Michigan during the trapping season 1938-39 were parasitized by *D. renale.* Benbrook (1940) reported the mink as a host of *Dracunculus medinensis,* in Iowa. In two papers (1941a, b) Morgan listed the nematodes of the subfamily Physalopterinae known to parasitize North American vertebrates; and in 1943, he reported *Molineus patens* from the mink. Beaver (1941) in his life history study of the fluke, *Euparyphium melis,* reported the mink as a natural host in Michigan. Goble (1942) recovered the nematodes, *Skrjabingylus nasicola* and *Filaroides bronchialis* (= *martis*), from mink in New York. Sealander (1943) in Michigan examined 32 wild-caught minks in 1940 and 126 in 1941. The incidence of parasitism by five species of helminths is given for the two years. Finally, Cameron (1944) suppressed the name, *Parametorchis canadensis,* as a synonym of *Metorchis conjunctus* of Cobbold.

Helminths of Weasels.—Swales' (1933) review of Canadian helminthology contains much of the information on helminths of fur-bearing animals examined in Canada and published up to that time. Swales (1938) reported the nematode, *Skrjabingylus nasicola,* from the frontal sinuses of the short-tailed weasel, *Mustela erminea cicognanii.* An examination of 426 skulls of Mustelidae in the National Museum of Canada revealed that "41 or 9.7 per cent showed obvious lesions of parasitic infestation of the frontal sinuses." Skulls showing lesions were *M. e. cicognanii, M. e. arctica, M. frenata longicauda,* and *M. f. frenata.* Worms were recovered only from *M. e. cicognanii.* Goble and Cook (1942) do not believe that enlargements or abnormalities of the sinuses are a good index of the incidence of *S. nasicola.* Goble (1942) reported the Guinea worm from the short-tailed weasel in New York. Morgan

(1943) recovered *Physaloptera maxillaris* from the short-tailed, the long-tailed, and the least weasels. Also from the least weasel he reported the nematode, *Soboliphyme baturini*. Swanson and Erickson (1946) reported *Alaria taxideae* from the short-tailed and long-tailed weasels in Minnesota. Hall and Dougherty (in press) examined several hundred weasel skulls for evidence of skrjabingyliasis.

Helminths of Skunks.—In a study of the food habits of fur-bearing animals in California, Dixon (1925) examined twenty skunks and stated that 10.4 per cent of the stomach contents were parasitic worms. Although the worms were not identified, it is possible that they were *Physaloptera*. Dikmans (1931) reported the hookworm, *Uncinaria* sp., from the large striped skunk, and Skinker (1935) described the cestode, *Oochoristica mephitis*, from the same host. Hamilton (1936), in a study of the food habits of the large striped skunk in New York, examined 1,067 stomachs. Ninety-six per cent contained the roundworm, *Physaloptera maxillaris*. Grinnell, Dixon, and Linsdale (1937) found nematodes, probably a filarid species, in the large striped skunk. They described the infection thus: "The worms were on the upper parts of the hind legs, on the back, and around the shoulders. Sometimes they were in bunches, very long, and as thin as a thread." The same authors found nematodes (probably *Skrjabingylus chitwoodorum*) in the frontal sinuses of a little spotted skunk.

Swales (1938) reported obvious lesions of parasitic infestations of the frontal sinuses of skulls of the large striped and the little spotted skunks in the collection of the National Museum of Canada. No worms were recovered. Hill (1939) described *Skrjabingylus chitwoodorum* from the same hosts. Also in 1939, Perry described the cestode, *Oochoristica oklahomensis*, from the little spotted skunk. Stegeman (1939) reported that 90 per cent of the large striped skunks that he examined in New York contained *Ascaris columnaris;* 50 per cent, *Anoplocephala* sp.; and five per cent, *Physaloptera maxillaris*. Leigh (1940) reported *Oochoristica mephitis*, and *Physaloptera turgida* from large striped skunks in Illinois. Morgan (1941b) restudied Leigh's specimens of *Physaloptera* and stated that they are the species *maxillaris*. In 1941, Wallace described the lung worm, *Crenosoma microbursa*, from the large striped skunk in Minnesota, and Cowan (1941) reported *Skrjabingylus chitwoodorum* from the spotted skunk in British Columbia. Hobmaier (1941a) described *Crenosoma mephitidis* from the large striped and little spotted skunks in California. From the same hosts Hobmaier (1941c) reported *Skrjabingylus chitwoodorum*. In 1942, Goble reported *S. chitwoodorum* from skunks in New York and described the nematode, *Crenosoma zederi*. Bell and Chalgren (1943) reported *S. chitwoodorum* from the skunk in Pennsylvania. Dougherty (1945) synonymized *C. zederi* with *C. mephitidis* of Hobmaier. Tiner (1946) recorded for the first time *Filaria martis* and *Molineus* sp. from skunks in Texas.

Helminths of Sea Otter, Otter, and Wolverine.—The only record of parasites from the sea otter that I have been able to find is that of Barabash-

Nikiforov (1935) who examined two animals from the Commander Islands, Alaska. Both of the otters contained nematodes, *Porrocaecum decipiens,* and cestodes that could not be identified. In 1938, McIntosh described *Taenia twitchelli* from an Alaskan wolverine. The larval stage of this tapeworm occurs in the lungs of the porcupine, *Erethizon epixanthum.* In 1940, McIntosh described the fluke, *Diplostomum fosteri,* from the Panama otter, *Lutra repanda.* From the same host he recovered the fluke, *Phagicola longa.* Beaver (1941) found that the otter served as a host for the fluke, *Euparyphium melis,* in Michigan.

Helminths of Marten, Fisher, and Badger.—In 1932, Chitwood reported *Uncinaria stenocephala* from a fisher taken in Quebec. In 1935, Skinker described *Taenia taxidiensis* from a badger, and in 1937, Honess described a new genus and species of cestode, *Fossar angertrude,* from the same host. Herman and Goss (1940) reported trichinosis in a badger from the New York Zoological Park. This is the second record of *T. spiralis* in this species. Bezdek (1942) summarized the available information on the nematode, *Soboliphyme baturini,* a parasite of Siberian and American martens. Marshall (1942) studied 107 marten carcasses from Idaho. Forty-two were examined grossly for parasites. Six contained *Ascaris columnaris,* and one, *S. baturini.* Morgan (1943) reported *S. baturini* from the marten and fisher, and *A. columnaris* (?) from the badger.

Source of Material

Most of the mustelids on which this report is based were collected in the wild in Minnesota from 1932 to 1944. They represent ten species as follows: mink (*Mustela vison*), 151 specimens of which 72 were fur farm animals; short-tailed weasel (*Mustela erminea cicognanii*), 322 specimens of which 88 were without stomachs, one without intestines, and 37 had neither intestines nor stomachs; long-tailed weasel (*Mustela frenata*), 21 specimens; least weasel (*Mustela rixosa*), one specimen; striped skunk (*Mephitis mephitis*), 15 specimens of which six were without stomachs; spotted skunk (*Spilogale putorius*), 24 specimens of which ten were without stomachs and one without intestines; badger (*Taxidea taxus*), eight specimens two of which had been in captivity for two years; otter (*Lutra canadensis*), 3 specimens; and one specimen each of marten (*Martes americana*) and fisher (*Martes pennanti*). Most of the animals had been skinned but otherwise were entire except as noted above.

Parasites Recovered from the Hosts

Twenty-four species of helminths were recovered from the 547 mustelids examined. The percentage of hosts infected by each species of parasite is based on the parts of the host that were available for study. No parasites were found in the otter, marten, fisher, and least weasel. In some cases, because of the condition of the parasites, it was not possible to determine them to species. The data on infections, summarized in Table No. 1, indicate that the six parasites which occurred most commonly were *Alaria taxideae, Euparyphium*

melis, Mesocestoides latus, M. variabiles, Ascaris columnaris, and *Physaloptera maxillaris.* Although the remaining 18 species occurred more rarely, multiple infections of parasites occurred in about 40 per cent of the hosts.

Alaria taxideae, an apparently undescribed species which has a wide host distribution in mustelid mammals in Minnesota, has recently been described by Swanson and Erickson (1946).

Parasites of Mustelidae in Relation to Food Habits

All of the flukes listed in Table No. 1 require intermediate hosts (snails, frogs, and/or mammals) to complete their life cycles. Many of these hosts are regularly utilized by various species of mustelids for food. The flukes found most consistently in wild-caught Minnesota mustelids were *Alaria mustelae, A. taxideae, Euparyphium melis, Paragonimus kellicotti,* and *Sellacotyle mustelae.* The larval stages of these flukes occur respectively in fish and meadow mice; unknown, but possibly the same as for *A. mustelae;* crayfish and frogs; crayfish; and fish.

The larval stages of the tapeworms listed in Table No. 1 are unknown except for *Taenia tenuicollis* which, according to Skinker (1935c) occurs in muskrats, a favorite prey species of the mink, which harbors the adult form.

Some of the nematodes listed in Table No. 1 require or are thought to require intermediate hosts. The larva of *Dracunculus medinensis* occurs in various species of *Cyclops;* that of *D. insignis* probably does also. The primary host becomes infected by drinking water containing infected *Cyclops.* Infections of kidney worm, *Dioctophyma renale,* in carnivores results from eating fish harboring larvae in their mesentaries (Woodhead, 1945). Roundworms of the genus *Physaloptera* are believed to pass the larval stage encysted in insects. Also, they have been found in the muscles of ruffed grouse and weasels. It is possible that these species may serve as transport hosts for *Physaloptera* larvae and that skunks, minks, and badgers become infected either by eating infected insects or infected transport hosts.

Petrov and Gugarin (1937) have shown that *Filaroides martis* and *Skrjabingylus nasicola* require gasteropod molluscs as intermediate hosts; they conducted experimental work on the polecat, a Eurasiatic mustelid. Hobmaier (1941) has shown that *Skrjabingylus chitwoodorum* also requires gasteropod intermediate hosts.

TABLE 1.—Helminth Parasites Recovered from 547 Wild-caught Minks, Weasels, Skunks, and Badgers.

Name of Parasite	Organ	Possibilities of Parasite Occurring*	Times Parasite Occurred	Hosts	Percentage of Hosts Infected
Trematodes or Flukes					
Alaria taxideae	Sm. Intestine	284	39	*Mustela e. cicognanii*	13.7
	Sm. Intestine	21	12	*Mustela frenata*	57.1
	Sm. Intestine	23	12	*Spilogale putorius*	52.1
	Sm. Intestine	15	4	*Mephitis mephitis*	26.6
	Sm. Intestine	8	1	*Taxidea taxus*	12.5
Alaria mustelae	Sm. Intestine	79	17	*Mustela vison*	21.5
	Sm. Intestine	284	4	*Mustela e. cicognanii*	1.4
	Sm. Intestine	23	1	*Spilogale putorius*	4.3
Euparyphium melis	Sm. Intestine	79	25	*Mustela vison*	31.6
	Sm. Intestine	284	1	*Mustela e. cicognanii*	0.3
Euparyphium sp.	Sm. Intestine	8	1	*Taxidea taxus*	12.5
Euryphelmis monorchis	Sm. Intestine	72	2	*Mustela vison***	2.7
Paragonimus kellicotti	Lungs	79	2	*Mustela vison*	2.5
	Lungs	72	1	*Mustela vison***	1.3
Metorchis conjunctus	Gall Bladder		1	*Mustela vison***	
Sellacotyle mustelae	Sm. Intestine	79	5	*Mustela vison*	6.3
Cestodes or Tapeworms					
Anoplocephalidae (ova)	Sm. Intestine	284	1	*Mustela e. cicognanii*	0.3
Mesocestoides latus?	Sm. Intestine	23	4	*Spilogale putorius*	17.4
	Sm. Intestine	15	1	*Mephitis mephitis*	6.6
Mesocestoides variabilis?	Sm. Intestine	23	3	*Spilogale putorius*	13.0
	Sm. Intestine	15	1	*Mephitis mephitis*	6.6
Mesocestoides sp.	Sm. Intestine	23	2	*Spilogale putorius*	8.7

* Based on portion of carcass available
** Fur Farm Animals

Name of Parasite	Organ	Possibilities of Parasite Occurring*	Times Parasite Occurred	Hosts	Percentage of Hosts Infected
Taenia tenuicollis	Sm. Intestine	72	2	*Mustela vison***	2.7
Taenia sp.	Sm. Intestine	284	1	*Mustela e. cicognanii*	0.3
Taenia sp.	Sm. Intestine	21	1	*Mustela frenata*	4.7
Nematodes or Roundworms					
Ascaris columnaris	Sm. Intestine	23	4	*Spilogale putorius*	17.4
	Sm. Intestine	8	1	*Taxidea taxus*	12.5
Capillaria sp.	Sm. Intestine	284	1	*Mustela vison*	0.3
	Sm. Intestine	72	4	*Mustela vison***	5.5
Dioctophyma renale	Kidney	72	5	*Mustela vison***	6.9
Dranunculus insignis?	Skin	15	1	*Mephitis mephitis*	6.6
Dranunculus medinensis	Hind leg	72	2	*Mustela vison***	2.7
Filaroides martis	Trachea	79	4	*Mustela vison*	5.0
	Trachea	72	7	*Mustela vison***	9.7
Molineus patens	Sm. Intestine	8	1	*Taxidea taxus*	12.5
Molineus? sp. (larvae)	Sm. Intestine	79	2	*Mustela vison*	2.5
	Sm. Intestine	284	13	*Mustela e. cicognanii*	4.5
	Sm. Intestine	21	1	*Mustela frenata*	4.7
Physaloptera maxillaris	Stomach	14	13	*Spilogale putorius*	92.8
	Stomach	9	4	*Mephitis mephitis*	44.4
	Stomach	8	1	*Taxidea taxus*	12.5
Physaloptera torquata	Stomach	8	1	*Taxidea taxus*	12.5
Physaloptera sp.	Stomach	79	1	*Mustela vison*	1.2
	Stomach	197	1	*Mustela e. cicognanii*	0.5
Skrjabingylus nasicola	Frontal Sinus	15	1	*Mustela e. cicognanii*	6.6
Spirurid (larvae)	Diaphragm	81	3	*Mustela e. cicognanii*	3.7
Acanthocephala or Thorny-headed Worms					
Moniliformis sp.	Sm. Intestine	284	5	*Mustela e. cicognanii*	1.7

* Based on portion of carcass available
** Fur Farm Animals

Helminths Reported from North American Mustelidae

MINK—*Mustela vison*

Trematodes or flukes.

**Alaria freundi* Sprehn, 1932 (55)[2]
** **Alaria mustelae* Bosma, 1931 (1, 10, 11)
†*Dicrocoelium dendriticum* (Rudolphi, 1818) Looss, 1899
†*Distoma* sp.
**Euparyphium inerme* (Fuhrmann, 1904) (1, 37, 49, 57)
** **Euparyphium melis* (Goeze, 1782) Dietz, 1909 (1, 6, 37)
** **Euryhelmis monorchis* Ameel, 1938 (4)
**Euryhelmis squamula* (Rudolphi, 1819) Poche, 1925 (42)
** * †*Paragonimus kellicotti* Ward, 1908 (50)
**Paragonimus* sp. (59)
** * †*Metorchis conjunctus* (Cobbold, 1860) Cameron, 1944 = *Parametorchis canadensis* Price, 1929 (1, 28, 37)
**Plagiorchis proximus* Barker, 1915 (57)
** **Sellacotyle mustelae* Wallace, 1935 (60)
†*Troglotrema* [= *Nanophyetus*] *salmincola* (Chapin, 1926) Witenberg, 1932

Cestodes or tapeworms.

†*Mesocestoides litteratus* (Batsch, 1786) Dolley, 1894
** **Taenia tenuicollis* Rudolphi, 1819 (54)

Nematodes or roundworms.

**Ascaris* sp. (1, 37, 57)
** **Capillaria* sp. (1, 37, 50, 57)
** * †*Dioctophyma renale* (Goeze, 1782) Balbiani, 1869 (1, 24, 37, 50, 57, 62)
** **Dracunculus mediensis*[3] (Linnaeus, 1758) Gallandant, 1773 (8, 15)
†*Filaria muscularis* (Walton, 1927) Walton, 1928
* †*Filaria* sp. (1, 37, 57)
** **Filaroides martis* (Werner, 1782) Dougherty, 1943 (1, 23, 37, 57)
* †*Gnathostoma spinigerum* Owen, 1838 (28)
**Molineus patens* (Dujardin, 1844) Skriabin and Shul'ts, 1926 (47, 51)
***Molineus* sp.
**Physaloptera maxillaris* Molin, 1860 (45)
** **Physaloptera* sp. (47)
**Skrjabingylus nasicola* (Leuckart, 1842) Petrov, 1927 (23, 28, 50)
**Strongyloides* sp. (1, 37, 57)
**Trichinella spiralis* (Owen, 1835) Railliet, 1895 (28)

SHORT-TAILED WEASEL—*Mustela erminea cicognanii*

Trematodes or flukes.

***Alaria mustelae* Bosma, 1931
** ***Alaria taxideae* Swanson and Erickson, 1946 (58a)
***Euparyphium melis* (Goeze, 1782) Dietz, 1909

Cestodes or tapeworms.

**Anoplocephalidae (ova in feces)
***Taenia* sp.

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* Recorded by various authors since Stiles and Baker (1935).
** New record; see the present paper.
† Species recorded by Stiles and Baker; includes records up to about 1930.
[2] Numbers in parenthesis refer to authors in the bibliography who reported the parasite from the host in question.
[3] Chandler (1942) tends to consider the *Dracunculus* reported from North American mammals as the species *insignis* rather than *medinensis*.

* Based on portion of carcass available
** Fur Farm Animals

Nematodes or roundworms.
Dracunculus medinensis (Linnaeus, 1758) Gallandant, 1773 (20)
**Molineus patens* (Dujardin, 1844) Skriabin and Shul'ts, 1926
**Physaloptera maxillaris* Molin, 1860 (47)
** *Physaloptera* sp. (46)
** *Skrjabingylus nasicola* (Leuckart, 1842) Petrov, 1927 (16, 58)
**Spirurid (larvae encysted in diaphragm)

Acanthocephala or thorny-headed worms.
**Moniliformis* sp.

LONG-TAILED WEASEL—*Mustela frenata*

Trematodes or flukes.
** *Alaria taxideae* Swanson and Erickson, 1946 (58a)

Cestodes or tapeworms.
**Taenia* sp.

Nematodes or roundworms.
**Filaroides martis* (Werner, 1782) Dougherty, 1943 (23)
**Molineus* sp.
**Physaloptera maxillaris* Molin, 1860 (47)
**Physaloptera* sp. (46)
**Skrjabingylus nasicola* (Leuckart, 1842) Petrov, 1927 (23)

LEAST WEASEL—*Mustela rixosa*

Nematodes or roundworms.
**Molinens patens* (Dujardin, 1844) Skriabin and Shul'ts, 1926 (47)
**Physaloptera maxillaris* Molin, 1860 (47)

LARGE STRIPED SKUNK—*Mephitis mephitis*

Trematodes or flukes.
** *Alaria taxideae* Swanson and Erickson, 1946 (58a)
**Sellacotyle mustelae* Wallace, 1935 (60, experimental)

Cestodes or tapeworms.
**Anoplocephala* sp. (56)
†*Mesocestoides latus* Mueller, 1927
***Mesocestoides latus*?
†*Mesocestoides variabilis maior* Mueller, 1928
***Mesocestoides variabilis*?
***Mesocestoides* sp. (58b)
**Oochoristica mephitis* Skinker, 1935 (52)
†*Taenia* sp.

Nematodes or roundworms.
*†*Ascaris columnaris* Leidy, 1856 (56)
†*Ascaris dasypodina* Baylis, 1922
†*Ascaris* sp.
**Crenosoma mephitidis* Hobmaier, 1941 (31, 34)
**Crenosoma microbursa* Wallace, 1941 (61)
***Dracunculus insignis*?
†Eunematoda
**Filaria martis* Gmelin, 1790 (58b)
**Molineus* sp. (58b) (possibly from *Mephitis*)
*Nematode (*Filaria*? sp.) (26)
** * †*Physaloptera maxillaris* Molin, 1860 (27, 32, 39, 45, 56, 58b)
**Skrjabingylus chitwoodorum* Hill, 1939 (7, 19, 23, 30, 33)
†*Strongyloides papillosus* (Wedl, 1856) Ransom, 1911
**Uncinaria* sp. (17)

Acanthocephala or thorny-headed worms.
**Acanthocephala* sp. (58b)

HOODED SKUNK—*Mephitis macroura*
Nematodes or roundworms.
**Physaloptera maxillaris* Molin, 1860 (45)

HOG-NOSED SKUNK—*Conepatus mesoleucus*
Nematodes or roundworms.
**Filaria martis* Gmelin, 1790 (58b)
**Physaloptera maxillaris* Molin, 1860 (45)
Acanthocephala or thorny-headed worms.
**Acanthocephala* sp. (58b)

PRAIRIE SPOTTED SKUNK—*Spilogale putorius*[4] and related forms
Trematodes or flukes.
** **Alaria taxideae* Swanson and Erickson, 1946 (58a)
Cestodes or tapeworms.
***Mesocestoides latus*?
†*Mesocestoides variabilis* Mueller, 1927
***Mesocestoides variabilis*?
***Mesocestoides* sp.
**Oochoristica oklahomensis* Perry, 1939 (48)
Nematodes or roundworms.
***Ascaris columnaris* Leidy, 1856
**Crenosoma mephitiditis* Hobmaier, 1941 (31)
** **Physaloptera maxillaris* Molin, 1860 (32, 45, 58b)
** **Skrjabingylus chitwoodorum* Hill, 1939 (16, 30, 33)
Acanthocephala or thorny-headed worms.
**Acanthocephala* sp. (58b)

OTTER—*Lutra canadensis*
Trematodes or flukes.
**Euparyphium melis* (Goeze, 1782) Dietz, 1909 (6)
Nematodes or roundworms.
**Physaloptera* sp. (46)

PANAMA OTTER—*Lutra repanda*
Trematodes or flukes.
**Diplostomum fosteri* McIntosh, 1939 (44)
**Phagicola longa* (Ransom, 1920) Price, 1932 (44)

WOLVERINE—*Gulo luscus*
Trematodes or flukes.
†*Opisthorchis felineus* (Rivolta, 1884) Blanchard, 1895
Cestodes or tapeworms.
†*Bothriocephalus* sp.
**Taenia twitchelli* Schwartz, 1924 (43)
Nemotodes or roundworms.
†*Dioctophyme renale* (Goeze, 1782) Balbiani, 1809
* †*Soboliphyme baturini* Petrov, 1930 (9)

MARTEN—*Martes americana*
Nematodes or roundworms.
**Soboliphyme baturini* Petrov, 1930 (9, 47)

MARTEN—*Martes caurina*
Nematodes or roundworms.
**Ascaris columnaris* Leidy, 1856 (41)
**Soboliphyme baturini* Petrov, 1930 (9, 41, 47)

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4 According to Hall (1936) it is probable that many of the spotted skunks (*S. interrupta, S. gracilis, S. phenax,* and *S. latifrons*) now accorded full specific rank will all be reduced to the species *putorius* eventually.

FISHER—*Martes pennanti*

Nematodes or roundworms.
**Soboliphyme baturini* Petrov, 1930 (47)
**Uncinaria stenocephala* (Railliet, 1884) Railliet, 1885 (14)

BADGER—*Taxidea taxus*

Trematodes or flukes.
** **Alaria taxideae* Swanson and Erickson, 1946 (58a)
***Euparyphium* sp.

Cestodes or tapeworms.
**Fossor angertrudae* Honess, 1937 (35)
**Taenia taxidiensis* Skinker, 1935 (53)
†*Taenia* sp.

Nematodes or roundworms.
***Ascaris columnaris* Leidy, 1856
**Ascaris* sp. (47, 57)
***Molineus patens* (Dujardin, 1844) Skriabin and Shul'ts, 1926
†*Monopetalonema eremita*[5] Leidy, 1886
** **Physaloptera maxillaris* Molin, 1860 (45)
** * †*Physaloptera torquata* Leidy, 1886 (45, 47)
**Physaloptera* sp. (57)
* †*Trichinella spiralis* (Owen, 1835) Railliet, 1895 (29)

SEA OTTER—*Enhydra lutris*

Cestodes or tapeworms.
**Cestode* sp. (5)

Nematodes or roundworms.
**Porrocaecum decipiens* (Krabbe, 1878) Krabbe, 1878 (5)

Keys to the Helminths of North American Mustelidae

TREMATODA

1. Body divided into a fore body bearing the organs of attachment and a hind body bearing the sex organs 2
   Body not divided into two parts 5
2. Vitellaria occurring in both the fore body and hind body ..... *Diplostomum fosteri*
   Vitellaria confined to the fore body 3
3. Pharynx large, 133 to 240 μ long by 114 to 190 μ wide; average 172 x 147 μ. Posterior testis horseshoe-shaped ..... *Alaria taxideae*
   Pharynx smaller. Posterior testis not horseshoe-shaped 4
4. Pharynx 70 to 120 μ by 40 to 108 μ, in the mean twice as long as the oral sucker which is subequal to the ventral sucker. Ovary usually on the left ..... *Alaria freundi*
   Pharynx 71 to 120 μ by 62 to 116 μ, in the mean 1 3/10 times as long as the oral sucker which is larger than the ventral sucker. Ovary always on the right ..... *Alaria mustelae*
5. A collar of spines around the oral sucker. Testes tandem and parallel to length of body 6
   No collar of spines around the oral sucker, or if present testes tandem and parallel to width of body 7
6. Body length 14 mm. Eggs 80 x 50 μ ..... *Eurparyphium inerme*
   Body length 3.86 to 10.5 mm. Eggs 117 to 130 μ by 72 to 84 μ ..... *Euparyphium melis*
7. In the bile ducts or gall bladder 8
   In the lungs or intestines 9

[5] This species is not keyed out because there is no adequate description of it.

8. Length 1.7 to 2 mm. Vitelline gland and loops of uterus extending anterior of the acetabulum. In the gall bladder ..... *Metorchis conjunctus*
Length 7 to 12 mm. Vitelline gland and loops of uterus not extending anterior of acetabulum. In the bile ducts, occasionally the intestine ..... *Opistorchis felineus*
9. In the lungs ..... *Paragonimus kellicotti*
In the intestines 10
10. Prepharynx very long, 104 to 370 μ. Circumoral spines present ..... *Phagicola longa*
Prepharynx very short or absent. Circumoral spines absent 11
11. Total length 1.32 to 1.98 mm. Testes placed obliquely one behind the other ..... *Plagiorchis proximus*
Total length 1.1 mm. or less. Testes situated laterally, when both are present 12
12. Body wider than it is long 13
Body longer than it is wide 14
13. Length 0.60 mm. width 1.45 mm. Both testes present ..... *Euryhelmis squamula*
Length 0.44 mm., width 0.61 mm. Only one testis present, or male genital system lacking ..... *Euryhelmis monorchis*
14. Length 0.8 to 1.1 mm. Intestinal ceca pass around the acetabulum and between the testes; cirrus pouch present ..... *Troglotrema salmincola*
Length 0.33 mm. Intestinal ceca reach only to middle of acetabulum; cirrus pouch absent ..... *Sellacotyle mustelae*

CESTODA

1. Scolex with two elongated slit-like suckers ..... *Diphyllobothrium* sp.
Scolex with four rounded suckers 2
2. Scolex without rostellum or hooks 3
Scolex with rostellum and hooks 8
3. Genital pores on ventral surface of segment, median 4
Genital pores lateral 6
4. Scolex 350 μ in diameter. Testes 40 to 45. Eggs 22 μ in diameter ..... *Mesocestoides variabilis*
Scolex 550 to 750 μ in diameter 5
5. Scolex 550 to 600 μ in diameter. Testes 30 to 45. Egg 25 to 35 μ in diameter ..... *Mesocestoides litteratus*
Scolex 550 to 750 μ in diameter. Testes 27 to 30. Eggs 22 to 25 μ in diameter ..... *Mesocestoides latus*
6. Uterus persistent developing by outpocketing; no egg capsules; genital pores unilateral ..... *Anoplocephala* sp.
Uterus breaks down into egg capsules; genital pores irregularly alternate 7
7. Strobila 11-25 mm. long. Cirrus pouch 55-65 μ long. Testes 44-47. Egg 30 μ in diameter ..... *Oochoristica mephitis*
Strobila 29-124 mm. long. Cirrus pouch 68-85 μ in diameter. Testes 37-46. Eggs 36-47 μ in diameter ..... *Oochoristica oklahomensis*
8. Rostellum with a single row of 22-25 hooks. Hooks 83-99 μ long. Suckers 192-239 μ in diameter. Uterine branches 11-23 ..... *Fossor angertrudae*
Rostellum apparently with a double row of hooks 9
9. Only the large hooks known. Hooks 90-93 μ long; handle about 56 μ long; guard 44-47 μ long. Suckers 140 μ in diameter ..... *Taenia taxidiensis*
Both large and small hooks known 10
10. A double row of 30-36 suckers; large hooks 195 μ long; small hooks 155 μ long. Suckers about 215 μ in diameter ..... *Taenia twitchelli*
A double row of 42-60 hooks. Large hooks 16-24 μ long; small hooks 13-21 μ long. Sucker about 77-110 μ in diameter ..... *Taenia tenuicollis*

NEMATODA

1. Adult worms parasitic in the intestinal tract and in various organs 3
Larval worms encysted in the voluntary muscles 2
2. Cysts lemon shaped, considerably longer than wide. Larva tightly coiled, frequently from both ends. Tail of larva blunt ..... *Trichinella spiralis*

Cyst rounded, almost as wide as long. Larva loosely coiled in one direction. Tail of larva conical ..... spiruride, probably a physalopterid

3. Probably no parasitic males; parasitic females not over 6 mm. long; uteri with 12-15 mature eggs ..... *Strongyloides papillosus*
Parasitic males and females; latter with more than 12-15 eggs in uteri 4

4. Esophagus consisting of a narrow tube running through the center of a row of single cells 5
Esophagus not consisting of a narrow tube running through the center of a row of single cells 6

5. Worms small, just visible to naked eye, viviparous ..... *Trichinella spiralis*
Worms large, readily visible to naked eye, oviparous ..... *Capillaria* sp.

6. Males with a bursa copulatrix (bursa may be vestigial as in *Filaroides martis*, which occurs in cysts in the lungs, or strongly reduced as *Skrjabingylus chitwoodorum* and *S. nasicola*, which occur in the frontal sinuses) 7
Males without a bursa copulatrix 15

7. Bursa copulatrix cuticular and supported by rays. Eggs usually thin-shelled 9
Bursa copulatrix muscular and not supported by rays. Eggs thick-shelled and the surface covered with depressions 8

8. Head not enlarged. In the kidney or body cavity ..... *Dioctophyma renale*
Head enlarged having the form of a sucker. In the stomach or intestine ..... *Soboliphyme baturini*

9. Parasites of the alimentary canal 10
Parasites of the respiratory system 11

10. Stout worms with the buccal capsule well developed. Oral aperture guarded by a pair of plate-like cutting organs and a pair of subventral lancets ..... *Uncinaria stenocephala*
Filiform worms with the buccal capsule feebly developed; cutting organs absent; head enlarged due to inflation of the cuticle ..... *Molineus patens*

11. Bursa copulatrix poorly to fairly well developed, supported by typical rays. Cuticle armed along the anterior part of the body with a series of rings composed of minute spines 12
Bursa copulatrix vestigial consisting of a cuticular extension. Cuticle not armed by a series of rings composed of spines 13

12. Bursa strongly reduced, much shorter than spicule; rays very short and stubby ..... *Crenosoma microbursa*
Bursa large and full, almost as long as spicule; rays well developed and digitiform ..... *Crenosoma mephitidis*

13. In cysts in the lungs ..... *Filaroides martis*
In the frontal sinuses of the skull 14

14. Males 13 to 17 mm. long; females 23-29 mm. long. Spicules 540 to 710 μ long; gubernaculum 72 to 88 μ long ..... *Skrjabingylus chitwoodorum*
Males 7.25 to 13 mm. long; females 10 to 18 mm. long. Spicules 164 to 175 μ long; gubernaculum 40 μ long ..... *Skrjabingylus nasicola*

15. Head with 3 large lobes or lips. Relatively stout worms 16
Head without 3 large lips, but with 2 lateral lips or lips absent. Relatively slender worms 18

16. Alimentary canal simple, without a postoesophageal ventriculus 17
Alimentary canal not simple, with a postoesophageal ventriculus. In the sea otter ..... *Porrocaecum decipiens*

17. Spicules 400 μ long; 36 pairs preanal papillae; 5 pairs postanal papillae ..... *Ascaris columnaris*
Spicules 1250 μ long; 33 pairs preanal papillae; 9 pairs postanal papillae ..... *Ascaris dasypodina*

18. Cephalic collarette or cuticular head bulb present. Parasites of the stomach 19
Cephalic collarette or cuticular head bulb absent. Parasites of the muscles 21

19. Cuticular head bulb present. Mouth with two large lateral trilobed lips bearing tooth-like ridges ..... *Gnathostoma spinigerum*
Cephalic collarette present. Mouth with large simple triangular lips armed with one or more teeth 20

20. Female with 2-A uteri (uterine branches dividing from a narrow neck which extends from the body of the uterus). Left spicule of male 612 to 1200 μ long; right spicule 437 to 735 μ long ..... *Physaloptera maxillaris*
Female with 2-B uteri (uterine branches dividing directly from the body of the uterus). Left spicule of the male 604 to 931 μ long; right spicule 532 to 804 μ long ..... *Physaloptera torquata*
21. Females 17 to 19.3 mm. long. Vulva about 2 mm. from the anterior end ..... *Filaria muscularis*
Females much longer than 19 mm. 22
22. Females 32 to 120 cm. long. Head end-on view shows oral opening surrounded by an inner circle of 4 papillae ..... *Dracunculus mediensis*
Females less than 29 cm. long. Head end-on view with different papillae arrangement 23
23. Vulva close to mouth, almost terminal, posterior extremity acuminate, curved ventrad ..... *Filaria martis*
Vulva close to middle of body, bluntly rounded posterior end ..... *Dracunculus insignis*

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Book Reviews

FISHES AND SHELLS OF THE PACIFIC WORLD. By John T. Nichols and Paul Bartsch. The Macmillan Company, New York City, 1945. 201 pages, 83 text figures and 16 plates. $2.50.

In parts I and II of this attractive little book Mr. John T. Nichols, of the American Museum of Natural History, has tried to give Americans scattered over the Pacific some idea of the fishes they may meet. As there are several thousand species of fishes in the Pacific, it is evident that only a few of them can be mentioned in a small popular work.

Part I has a short chapter on the origin and distribution of Pacific fishes, followed by one on some of the different kinds of fishes occurring over the area from the Aleutians to the South Seas. Thirteen pages are given to sharks and rays and only 42 pages to the other kinds of fishes. As there are at least 40 times as many bony fishes as there are of sharks and rays in the Pacific, this does not seem to be a well balanced treatment.

Part II is devoted to Fishes of Particular Interest. A chapter on sharks and rays is followed by one on Important Fish Groups. Those given are herrings and their allies, anchovies, lizard fishes, butterfly and angel fishes, wrasses and parrot fishes, and the demoiselles or pomacentrids. The butterfly fishes, wrasses and parrot fishes, and pomacentrids are all beautiful or strikingly colored conspicuous fishes, and attract great attention. Why the lizard fishes, a small dull-colored group of no economic importance or interest to anglers should be included, when common fishes of real importance are omitted is not evident. A chapter on Peculiar Fishes includes a very few of the remarkable fishes of the Pacific. Those selected are the lancet-fish, seahorses and pipefish, threadfish, pilot fish, the remoras, the flying gurnard, the almost incredible mudskipper, the frogfishes and the mousefish. The last chapter is on the big game fishes that abound over the Pacific. Swordfish, sailfish, barracuda, and various carangids are abundant, widespread, and important. Sportsmen and every one who likes to go fishing will be interested in this chapter.

The illustrations are line drawings of many of the fishes mentioned. They are quite helpful, but are not all well selected. In speaking of the large and important group of food fishes known as the sea basses, a figure is given of *Pseudanthias kelloggi*, a deep water Hawaiian fish known only from ten specimens; a figure of *Epinephelus merra*, found on every reef throughout the tropical Pacific except the Hawaiian area, would have been more useful.

To write a satisfactory work on the fishes of the Pacific within the limits of 118 small pages, is an impossible task, and the author has done as well as could be expected with such a terrible handicap. If another edition is called for a better job could be done by dividing the field between two books, one for the region between California and Japan and northward, the other devoted to the fishes of the tropical Pacific.

Part III, by Dr. Paul Bartsch, is a brief but very well coordinated treatment of the mollusks of the Western Pacific. A short discussion of mollusks in general, their occurrence and distribution, is followed by a systematic account of those in the tropical western Pacific. Since there are very many thousands of species in the area, only the more conspicuous and interesting kinds likely to be seen by visitors are briefly treated. Special attention is paid to the freshwater snails that are hosts to liver flukes and lung flukes, which infest tens of millions of people in the lands about the Western Pacific. Brief instructions for collecting mollusks are followed by a valuable list of reference works on Pacific mollusca. Sixteen plates, with 138 figures of mollusks, conclude the work, and will enable one to name the prominent shells found in the tropical Western Pacific.

There are very few errors, typographical or otherwise. On page 142 Panopea is called geoduck instead of goeduck. On page 48 the word Greelings should be Greenlings.—ALBERT W. C. T. HERRE, Stanford University, California.

ENTOMOLOGY FOR INTRODUCTORY COURSES. By Robert Matheson. Comstock Publishing Company. Ithaca, N. Y. 1944. Pp. xiv+600. 500 figs. $5.50.

As Professor Matheson has emphasized in the title, this book was written especially for the student entering his first course in Entomology. Topically it deals with the phylum of arthropods (25 pp.), the anatomy of insects with special emphasis on their mouthparts (2 chapters comprising 78 pages, of which 34 are devoted to mouthparts), the development and growth of insects (26 pp.), the classification of insects and the characteristics of members of most orders (364 pp.), and, finally, the relation of insects to human welfare (52 pp.). In addition there is a nine page glossary, a sixteen page bibliography of references of general or comprehensive nature, and a very extensive index of eighteen pages. The book is very attractively composed and excellently bound.

Matheson's expressed aim in presenting the subject matter of Entomology is to place emphasis on the biological aspects, especially "on the lives of these wonderful creatures." Although much attention is devoted to the life histories and habits of numerous insects, the reviewer is inclined to feel that the exposition of the biology of insects is unsatisfactory for a modern text. Little or no space is devoted to the physiology of insects, to the experimental analysis of insect embryology and behavior, to the cytology and histology of insects, and so on. Rather there is an extended but superficial account of classification, morphology and natural history of insects such as may be found in many of the older textbooks on the subject. Since most students entering a course in Entomology have had previous training in Biology, it is unfortunate that their biological knowledge is not built upon and expanded in such a work as this one.

The numerous illustrations are for the most part good, but one drawback lies in the fact that many of them (about 80) are the familiar, old and worn figures from the works of Professor Comstock. The text is not free from errors or careless statement, and some of these are rather surprising. For example, Matheson states that all arachnids are air-breathers; that crustaceans have at least five pairs of locomotory appendages; that "an adult insect never increases in size, however long it may live or however much food it may eat"; that "in North America there are not over twelve native species" of earwigs; and so forth. Certainly xiphosurans, halacarids, and others, obtain their oxygen by diffusion from water; ostracods may have but one or two pairs of locomotory appendages; *Meloe*, honey ant repletes, queen insects, some fleas, and others, may grow quite prodigiously after attaining the imaginal state; furthermore there are not less than forty species of earwigs in North America, although Matheson's figure is correct for the United States proper.

Nor is the glossary adequate, for it omits not a few of the technical terms used in the text (e.g.,—book lung, capitulum, crop, diapause, hypostome, parthenogenesis, pretarsus, etc.). The bibliography is also characterized by the omission of numerous desirable references. Perhaps the most surprising of the omissions, since the book stresses the life histories of insects, is the absence (except for "The Hunting Wasps") of Fabre's extensive and delightful works, so stimulating to students.

All in all Matheson's "Entomology for Introductory Courses" leaves much to be desired for the teaching of a modern course in Entomology. In the reviewer's opinion Imms' recent "Outlines of Entomology" is a much more satisfactory introduction, as is also Frost's "General Entomology." Still it is to be hoped that in the not distant future an Entomology will appear in the English language which will compare favorably with Weber's superb "Lehrbuch der Entomologie," or his "Grundriss" for introductory courses. —KENNETH W. COOPER, Princeton University, Princeton, N. J.

A BIBLIOGRAPHY OF THE HOMOPTERA (AUCHENORHYNCHA). By Zeno Payne Metcalf. North Carolina State College of Agriculture and Engineeering of the University of North Carolina, Raleigh, N. C. 10½ x 8½ inches. Vol. I—886 pp. Vol. II—186 pp. Cloth. $7.50 net.

This bibliography, composed of two volumes, treats the superfamilies Fulgoroidea and Cicadoidea of the Suborder Homoptera, series Auchenorhyncha. The first volume lists the authors alphabetically and their papers are listed chronologically by title with

place and date of publication. Some 8000 titles in all languages are listed which occur in about 1900 different publications. All titles are included up to June 1, 1942. An abstract note, often supplied by the author (bibliographer), is of great assistance in clarifying the contents of the article. Volume II lists the periodicals with places of publication and includes a topical index. This is especially useful both to students and specialists in the field of Homoptera in locating quickly papers dealing with certain specific fields, taxonomic or otherwise.

This impressive piece of work has been in preparation by Dr. Metcalf for some 30 years and is both accurate and complete. Bibliographies covering various fields of scientific work are essential and are invaluable to specialists in a particular field and to students of general scientific fields. This work will prove indispensable to the Homoptera specialist and a necessary reference volume for the library of entomology.

The enormous amount of work saved to the average student by a well organized reference list of this type can scarcely be estimated or appreciated. The reader is also the benefactor of a selection of references accomplished by Dr. Metcalf's intimate acquaintance with the field of the Homoptera, saving the time otherwise used in sifting out many unimportant or popular articles which do not contribute to information of a scientific nature or are not worth looking into to find out their contents.—DWIGHT M. DELONG, Ohio State University.

THE MICROBE'S CHALLENGE. By Frederick Eberson. The Jaques Cattell Press, Lancaster, Pa. 1941. 354 pp., frontispiece, 2 pls., 2 figs. $3.50.

It is seldom that an individual combines ability in science with the ability to write of scientific work in easily-read English. *The Microbe's Challenge* presents many technical principles, yet it moves along as spritely as a French novel. Something of the author's breezy style may be reevaled by the following quotations: ". . . As newer developments in the technique of staining gathered impetus from these masters, no privacy was left for microbes and their innocent secrets stood shamelessly revealed"; (p. 32) and, "For the development of his character Leeuwenhoek's long nose was an ideal affliction, because he wanted to see beyond it and he had to see far" (p. 24).

Although the author has carefully avoided scientific terminology he has managed to convey in everyday language a great deal of the foremost work in microbiology. Setting the stage in the first chapter with a general discussion of micro-organisms he proceeds in the second chapter with the historical development of bacteriology and the techniques of studying these organisms including staining, culture methods, and sterilization. In the following ten chapters the pertinent facts on many diseases are described with many interesting sidelights of historical interest. Among other topics the discussion of variability of microbes, on "chemical warfare" and on immunology are recommended in particular for excellence in presentation to the lay reader. The last twenty-one pages of the book include a glossary, an index and suggested readings.—NOE HIGINBOTHAM.